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THE PTEROPSIDA[1]

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(WITH PLATE XIII)

Two years ago, I published a reply to the various criticisms which had been made from time to time of the great group of vascular plants defined as Lycopsida. At that time a promise was made that the attacks, neither few nor unimportant, leveled at the pendent and corresponding phylum Pteropsida, would likewise be met. In the interval my time has been very much taken up with investigations on the higher seed plants, and it has heretofore been impossible to carry out the intention then expressed. The delay, however, is rather an advantage than otherwise, for it has enabled the opposition to the conceptions connected with the Pteropsida to crystallize and clarify, which materially simplifies the task of criticism. Moreover, in the past two years we have seen venerable but no longer useful morphological doctrines go by the board. Their disappearance is of importance in the present connection, because they have been haled into court in the present discussion.

The validity of the Pteropsida, as a natural phylum, may apparently now be taken as settled, since the group as defined by the present writer has been adopted by a number of botanists, whose knowledge, at once profound and extensive, of living and extinct vascular plants makes their opinion of the greatest weight. There appears accordingly to be no serious opposition at the present time to the conception that all those Vasculares which are

[1] Contributions from the Phanerogamic Laboratories of Harvard University, no. 30.

characterized by palingenetically large leaves and dorsal or abaxial sporangia are in reality so united by a common plexus of origin that they may be with advantage mustered under a common appelation.

Although the standing of the Pteropsida as a large natural phylum of plants now appears to be on a firm footing, the important question of the morphology of the central cylinder or stele of vascular plants is still the subject of much controversy, and the English school of morphologists, led by Dr. D. H. SCOTT, who is himself a host, has attacked the present writer's position with great vigor. The Pteropsida certainly are the appropriate battle ground for the decision of the fundamental morphological question of the internal morphology of the stem, since, unlike the Lycopsida, they are still in full vigor, while they share with the latter phylum the advantage of a very extended history. The most important line of attack is in connection with the morphological status of the pith, which the present writer regards as external tissue included by the stele in the course of evolution. The English anatomists, on the contrary, regard the pith as in all cases a specially differentiated central portion of the fibrovascular tissue itself. Of late, however, the extremity of the English view appears to be modified somewhat by the admission that in certain instances the pith may be derived from outside the stele. Another less important and not generally adopted criticism of the author's views is to the effect that the megaphyllous or large-leaved habit is not a primitive one for the Pteropsida. This criticism has been put forward by only a few of the English anatomists, and appears to have been effectually answered by two recent American writers on the subject.

The lapse of time has made the task of replying to criticisms against the extrastelar origin of the pith a much easier one. The growing-point hypothesis, which has been applied by STRASBURGER to the elucidation of the morphology of the pith, has been recently rejected by a number of morphologists in Europe and America.[2] The interpretation of the mature structure of the organs

[2] JEFFREY, E. C., Morphology and phylogeny. Science N.S. **23**:291. 1906.
BOWER, F. O., The origin of a land flora, chaps. xiv and xv. London. 1908.
COULTER, J. M., Vascular anatomy and the reproductive structures. Amer. Nat. **43**:219–230. 1909.

of the higher plants in reference to the so-called apical meristems has long dominated morphology of a certain type, although its validity in relation to the histological structure of stems, roots, etc., has never been admitted by such distinguished anatomists as DEBARY and VAN TIEGHEM. It has not been any gain to anatomy that STRASBURGER, a morphologist of the reproductive structures and the cell, should have forced the growing-point hypothesis into the anatomical field in his one important contribution to vegetative histology.[3] It is more unfortunate that his views have been adopted and elaborated by those who cultivate anatomy in England. With the overthrow of the hypothesis in regard to the morphological value of apical meristems, the views of the English anatomists, who have built on this uncertain foundation, have lost a fundamental support. That the application of the hypothesis of apical meristems to anatomical facts leads to hopeless contradictions and logical absurdities the present writer has shown in his article cited above. It appears to be unnecessary to repeat these arguments here.

It must be admitted that the English view, propounded by Dr. SCOTT in a review of the present author's investigations on the stele (*New Phytol.* 1902) and repeated with conviction by nearly all subsequent English writers on anatomical themes, has an air of probability in its favor, in spite of the fact that it can no longer summon to its support the hypothesis of the apical meristems. It seems prima facie improbable that the fibrovascular structures of the stem should be able to surround or contain tissues which primitively lie outside. Moreover, the holders of the view in regard to the stelar origin of the pith have the advantage that their opponents in a measure face the logical impossibility of proving a negative. Although it is not possible to prove in all cases that the pith may be derived from outside the stele, it is fortunately only necessary to demonstrate this in a few instances, in order to invalidate the position of those who claim that the pith is differentiated from the substance of the stele itself.

Professor GWYNNE-VAUGHAN among English anatomists is the one who has shown the greatest openness of mind in regard to the

[3] STRASBURGER, ED., Bau u. Verrichtungen d. Leitungsbahnen. Hist. Beitr. 3:1891.

origin of stelar structures, for, unlike most of his countrymen, he has always been willing to admit that there is some evidence as to the extrastelar origin of the pith in certain instances. To him belongs the credit of having called attention to the fact that in certain of the ferns, structures which are unquestionably extrastelar in their origin may penetrate the central cylinder of the stem.[4] Fig. 1 of the plate accompanying this article shows a transverse section of the stem of *Onoclea* (*Struthiopteris*) *germanica*. The stem is very irregular in outline on account of the crowded leaf bases attached to its surface. The leaf bases, actual or potential, are distinguishable by the fact that they have a double fibrovascular bundle. In the substance of the stem lie a number of cavities, situated for the most part within the boundaries of the central cylinder, as determined by a line drawn external to its bundles. These cavities are more or less occupied with a filmy substance representing the ramental covering of the epidermis. By inspection of the figure it can be clearly made out that the cavities plugged with *ramentum*, occurring in the substance of the pith, are derived from outside, and represent ingrowths of the external epidermis, including the outside air. Fig. 2 represents a part of a similar section somewhat more highly magnified. On the left may be seen the communication of the medullary pocket with the exterior surface of the stem. It is an axiom with the greater number of the English anatomists, that if pockets or apparent ingrowths of tissues, normally extrastelar, occur within the central cylinder, these are not what they appear to be, namely, incursions of extrastelar tissues into the substance of the stele, but, on the contrary, are merely portions of the stele which have been so transformed as to resemble tissues of the cortex. In the case supplied by our two figures we have a logical *reductio ad absurdum* of the usual English view, for here we have not only the external hairy covering of the stem but even the outside air making their way into the innermost sanctity of the stele. Even the most convinced adherent of the stelar origin of the pith must admit that in this case structures which are quite outside the stele

[4] GWYNNE-VAUGHAN, D. T., On the possible existence of a fern stem having the form of a lattice-work tube. New Phytol. **4**:no. 9. 1905.

are able to make their way into it. If it is once conceded that such clearly extrastelar substances as ramentum-covered epidermis and the free external atmosphere are able to make their way into the interior of the stele, there appears to be little ground for questioning that the cortex and its internal boundary, the endodermis, may penetrate the same *sanctum sanctorum*. In the present defunct condition of the growing-point hypothesis, it seems clear, in view of existence of such facts as those illustrated in the two figures just described, that the dogma of the stelar origin of the pith rests on an extremely weak foundation.

It is admitted further, even by those who are most extreme in their support of the view that the pith is always of stelar origin, that, although the central cylinder of the stem cannot include within itself the outlying tissues of the cortex, this possibility exists in the case of the leaf trace. Mr. BOODLE, the most logical and consistent of the younger English anatomists, and one whose contributions, together with those of Dr. D. T. GWYNNE-VAUGHAN, comprise the most important data on the anatomy of ferns which have recently appeared in England, not long since published an article on certain species of *Gleichenia*.[5] He here states that "the nearly circular or subcordiform petiolar bundle of *Eugleichenia* may be held to be derived from the horseshoe-shaped bundle of the *Mertensia* type by contraction, and by the fusion of the free ends of the horseshoe, *the sclerenchymatous cortex in the concavity of the latter thus becoming inclosed*, or at a higher level suppressed"! The present writer has italicized the significant part of the quotation. It is apparent that Mr. BOODLE admits that the foliar trace may include cortical tissue. If such an admission is made in the case of the Gleicheniaceae, it cannot fail of application to the petiolar structures of other families of ferns. Let us take as an example, among many others, the case of the Marattiaceae. In fig. 3 is represented the vascular system of the base of one of the large pinnules of *Angiopteris evecta*. The bundles are arranged in a horseshoe-shaped manner, with the two large bundles terminating the arms of the horseshoe turned inward and downward.

[5] BOODLE, L. A., and HILEY, W. E., On the vascular structure of some species of *Gleichenia*. Annals of Botany **23**:419–432. *pl. 29*. 1909.

Within this horseshoe-shaped cordon of bundles is inclosed a mass of cortical tissue, which to all intents is a pith. Fig. 4 represents a cross-section of the bundle system of the pinnular petiole at a higher level, where, as in *Gleichenia* cited above, the edges of the horseshoe have fused together. It is clear that as a result of this fusion we have a mass of included cortical tissue entirely surrounded by bundles, in other words a condition which the present writer has hypothetically considered to exist in the case of the central cylinder of the stem, where it contains a pith. On the right of the fused horseshoe-shaped complex of bundles two small strands are seen passing off to supply a pinnule of the second order, leaving a gap precisely like that found in connection with the departing leaf traces of the stem or main axis. It is impossible to disregard this obvious resemblance of all the structures in the petiole under discussion to those found in the stem. It is at once suggested that the interpretation of the two sets of facts must be the same, and that if, as is admitted, the petiolar strands are able to inclose tissues of the cortex, there is no reason to question that the same process of the inclusion of fundamental tissues by the fibrovascular system may take place in the stem. This view of the matter gathers force from the hypothesis, which has won favor in England and on the continent, that the leaf of ferns represents only a modified branch. If this view of the morphology of filicinean leaves is adopted, it makes the study of that organ of great use in throwing light on the conditions found in the stem, especially as the leaf by its well-recognized conservatism will supply us with evolutionary stages which have become obsolete in the stem proper.

Fig. 5 represents a cross-section of the entire rachis of *Marattia alata* at a point where the petiolar bundles have formed a closed system by the fusion of the originally free ends of the horseshoe-shaped complex. Here we see precisely the same conditions as are found in the case of *Angiopteris evecta*. Fig. 6 shows the same leaf axis at a higher point, where a vascular supply for a secondary axis is being given off. This plane of section is of special interest because the large medullary bundle formed from the fusion of the two margins of the original horseshoe-shaped complex is func-

tioning in the same way as is commonly found to be the case with the medullary strands of the stem, namely as a reparatory strand to help fill up the leaf gap above the point of departure of the traces. It is clear from what has been stated in the case of *Marattia alata*, just described, that the leaf may develop a vascular system resembling in a detailed manner that found in the case of siphonostelic stems. It seems eminently a sound conclusion to infer as a consequence, since the fundamental tissue of the cortex may readily be included in the fibrovascular system of the leaf trace, that a similar condition may also occur in the stem.

Only two examples have been chosen for illustration of the occurrence of siphonostelic leaf traces, but the genus *Danaea* among the Marattiaceae presents parallel conditions to *Angiopteris* and *Marattia*. Among the other families of ferns the phenomenon is frequently represented. A notable and common case is that of *Pteris aquilina*. Here the sides of the original channel-shaped leaf strand become strongly pushed in, and the fusion takes place so that the joining bundles constituting the margins of the fibrovascular complex of the leaf lie above and outside the siphonostelic lower part of the leaf system. The branches given off to the main ramifications of the leaf are derived from the lateral margins of the siphonostelic region, but in passing off receive a subtending strand from the large upper fused bundle, which lies on the outside of the stelar tube of the leaf axis. The siphonostelic condition in the foliar supply is not confined to the ferns, but is likewise of very frequent occurrence in the angiosperms, where it is susceptible of a similar morphological interpretation. In the case of certain dicotyledons, moreover, diverticula of the epidermis, lined with a hairy covering, make their way into the cavity of the pith of the leaf stalk, showing that here too there is no question of the possibility of extravascular tissues being included within the complex of bundles. It may be further stated that there appears to be no clear distinction between the condition where the cortical fundamental tissues become deeply embayed in the fibrovascular system of the leaf, and where an actual siphonostelic condition results from the fusion of the marginal bundles of the foliar complex. Accordingly it appears strictly logical to include

the deeply infolded petiolar supply of the cycads in our argument. Since the leaf traces of this group originate on the opposite side of the stem from that on which they pass out into their corresponding leaf, it would be necessary to assume that each half of the leaf supply carried with it its own peculiar portion of the medullary parenchyma, and that the fractions were accurately joined with one another in the leaf base, to the exclusion of the fundamental tissue of the cortex, if we were to accept the idea that the fibrovascular tissues are in general unable to embay or include portions of the fundamental tissues of the cortex. This seems much too improbable a supposition to be seriously entertained.

It appears evident, since the stelar system of the stem in the case of certain of the lower Pteropsida, for example, species of *Onoclea*, *Cystopteris*, *Aneimia*, etc., is able to include tissues and substances which are beyond question extrastelar in their origin, that no difficulty arises in regarding the pith present within the siphonostelic central cylinder of the lower (as well as the higher) Pteropsida as morphologically equivalent with the fundamental tissue of the cortex, with which it is often continuous through the gaps in the stelar walls resulting from the exit of the vascular supply of leaves and branches. A further argument in favor of this view is the frequent textural similarity between pith and cortex, even where the former as the result of upward evolutionary changes is no longer continuous with the fundamental tissue without the stele. It follows equally that the morphological doctrine for which STRASBURGER is responsible, and which has been carried to its logical conclusion and *reductio ad absurdum* by the English anatomists, namely, that the criteria of the morphological status of plant tissues are to be derived from a study of the growing point of the mature organ rather than from comparative anatomical considerations and particularly from a study of the seedling, falls to the ground.

It is now possible to consider with advantage the alleged primitive absence of foliar gaps in the Pteropsida, which has recently been asserted by GWYNNE-VAUGHAN in connection with studies on fossil representatives of the Osmundaceae. In the genus *Thamnopteris*, this author has found the center of the stele to be

occupied by a large mass of short tracheids, which he has interpreted as a pith of stelar origin. To state that a central mass of tissue, which according to the author's own admission is entirely tracheary, is the forerunner of the pith, and proves the origin of the latter from tissues of the stele, is apparently a clear case of begging the question. The example of another fossil osmundaceous genus, *Zalesskia*, which has also been brought into court by GWYNNE-VAUGHAN, is equally inconclusive, since the central tissues in the two species of this genus described are in a very bad condition of preservation. Naturally enough, in these obviously protostelic representatives of the Osmundaceae, this author found no evidence of the presence of foliar gaps. A much stronger argument in favor of his view is furnished by the fossil genus *Osmundites Dunlopi*. Here in sections of the very badly preserved stem it was impossible to distinguish clearly any foliar gaps. GWYNNE-VAUGHAN assumes that the obviously much contracted central cylinder of his *Osmundites Dunlopi* represents the primitive conditions in the Osmundaceae, and shows that foliar gaps were originally absent in this family. It is not less reasonable to suppose that the nearly contemporary *Osmundites skidgatensis* from the Lower Cretaceous of the western coast of the Dominion of Canada, in which the foliar gaps are very large and in which the pith very clearly communicates with the histologically strikingly similar tissues of the cortex, in reality represents the primitive condition for the Osmundaceae. All that the fossil evidence enables us to state regarding the Osmundaceae, which constitutes the only evidence for GWYNNE-VAUGHAN'S hypothesis of the original absence of foliar gaps in the fern series, is that the Osmundaceae varied more in structure in both directions during the Mesozoic than they do at the present time, in other words they presented a more generalized condition.

The evidence from the comparative anatomical and developmental standpoints is, on the contrary, clearly all in one direction. Mr. SINNOTT in a recent article[6] has shown that in the genus *Todea*, especially in the filmy subgenus *Leptopteris*, there is fre-

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quently an apparent absence of foliar gaps, but that in all the species which he studied in serial sections a gap was really present, although in a single section it might appear to be absent. Moreover, it was shown by this author that in the case of the horseshoe-shaped stele of the leaf in species of *Osmunda* and *Todea*, the passing off of the pinnular traces always left clear gaps in its wall. Moreover, both Mr. SINNOTT and Professor FAULL[7] have made it quite clear that the hypothesis of GWYNNE-VAUGHAN as to the primitive absence of foliar gaps in the Osmundaceae receives no support whatever from a consideration of the anatomy of the seedling of living species. Consequently, we may say of the hypothesis advocated by GWYNNE-VAUGHAN that it is not definitely confirmed by the fossil evidence, and that all the evidence derived from the consideration of the anatomy of the stem, leaf, and seedling of living species is entirely against his view. It may consequently be stated with confidence that at the present time there is no valid proof in favor of the original absence of foliar gaps in the Osmundaceae.

The English school of anatomists has been well advised in making its stand upon the stelar origin of the pith as opposed to its derivation by the inclusion of extrastelar fundamental tissue within the central cylinder, for if that view is once overthrown, a number of other conceptions commonly held in England fall with it to the ground. If it be clear that the pith is originally an inclusion of the fundamental tissues within the central cylinder, certain interesting conclusions immediately follow. One of the most important and far-reaching generalizations of modern plant anatomy, and one which receives the fullest support from the considerations of all the main groups of vascular plants, is that the foliar strand perpetuates the original condition of the wall of the stelar tube. There is distinct evidence in the case of the Osmundaceae, Ophioglossaceae, Lyginodendreae, Equisetales, etc., that the central cylinder of the stem was once composed of concentric fibrovascular bundles, since bundles of this type persist in the leaf trace or sporophyll trace of these various groups. This inevitably follows if it is admitted, as apparently it must be from

[7] FAULL, J. H., The stele of *Osmunda cinnamomea*. Trans. Canad. Inst. **8**:515–534. 1909.

the application of sound logic to the known facts, that the pith in these families or orders is morphologically included fundamental tissue.

On the basis of conclusions drawn from the leaf trace in existing pteridophytic groups, we must regard the concentric as the primitive type of fibrovascular bundle. This view of the matter is strengthened by the fact that the concentric bundle is characteristic of the phylogenetically older representatives of the Pteropsida. In the case of the Lycopsida, unfortunately, the evidence is very defective, since this phylum reached its culmination in the remote past and is now almost extinct. The English view of the matter is diametrically opposite, namely, that the collateral bundle is more ancient and that the concentric type has been derived from it. It has been cited in favor of this view, originally by Dr. SCOTT and afterward by nearly all the younger English anatomists, that no evidence is forthcoming in favor of the superior age of the concentric type of bundle in the case of the seedling of the ferns which have collateral stem bundles in the adult. This statement appears to be entirely fallacious. In the first place it would be just as reasonable to assume that centripetal or cryptogamic xylem was not originally present in the stem bundles of our existing gymnosperms, because forsooth it has never been found in the seedling stem. The present writer entirely agrees with the English anatomists in the conviction that centripetal xylem was once well developed in the stem of the ancestors of the living gymnosperms, but this conclusion rests on the persistence of this type of xylem in the leaf trace of forms actually living or their immediate ancestors. On the same basis of argument, concentric bundles were originally present in the stems of those few ferns which today show a collateral condition in their cauline system, for here, as in the gymnosperms, the structure of the leaf affords evidence which is no longer supplied by the seedling. Moreover, if the collateral type of bundle is really primitive for the fern series as a whole, one would expect to find some evidence of its presence in the seedlings of the extremely numerous modern ferns which are characterized by the presence of concentric bundles both in their stems and leaves. Although a great deal of attention has been devoted by

the younger English anatomists to hunting for such evidence in fern seedlings, success has not crowned their efforts. Moreover, if the collateral type of bundle really be primitive for the existing ferns, we should expect to find this condition present in the bases of their foliar organs. It follows, from all the considerations mentioned above, that the absence of the concentric condition in the seedlings of the comparatively few existing ferns showing collateral organization in their adult cauline system constitutes no valid argument against the primitiveness of the concentric bundle for the stem of these and of ferns in general. The evidence considered in connection with the extremely sound and satisfactory generalizations concerning the conservative character of the leaf trace, to which the English anatomists have contributed so honorable a share, is entirely in favor of the concentric as the primitive type of cauline bundle in the fern series.

It follows that none of the recent work overthrows the generalizations put forward in the writer's earlier memoirs as to the phylogeny of the stem in the vascular series. It now in fact appears much more clearly than formerly that the primitive condition of the vascular system in both stem and leaf in the Vasculares as a whole was what the present writer has designated protostelic, that is, a condition in which the fibrovascular tissues harbored no pith. Following this condition was one in which the fibrovascular system became transformed, especially in the more progressive stem, into a stelar tube lined both internally and externally with phloem and endodermis. In the process of time the internal phloem became degenerate, probably on account both of the absence of direct relation to the leaves and of the appearance of secondary growth, advantageously localized ultimately on the outer surface of the stele. The internal endodermis more slowly followed the internal phloem into oblivion, and is often found at the present time in the young individual where it is absent in the adult (Ophioglossaceae, Equisetaceae, Ranunculaceae). The pith must in all cases be regarded as a derivative of the cortex, which has become more or less completely sequestered within the stele. The tubular stele may with propriety and accuracy continue to bear the designation siphonostelic, a term moreover which, in addition to having

an apparently wider and truer significance than the English term solenostelic, holds the claim of priority.

NOTE ON THE LYCOPSIDA.—In the second edition of his admirable *Studies in fossil botany*, Dr. SCOTT adopts without question the present writer's phylum Pteropsida. He also adopts the designation Lycopsida, but confines its application to the Lycopodiales, living and extinct. For the remaining groups included in the present writer's Lycopsida, he proposes the name Sphenopsida, since he regards the Equisetales, Psilotales, and Sphenophyllales as not properly microphyllous, or to be included in the same phylum as the Lycopodiales. This view does not appear to be well founded, since the Equisetales and Psilotales are on anatomical grounds clearly and unquestionably microphyllous and likewise ventrisporangiate. There is no anatomical evidence as to the microphyllous character of the Sphenophyllales, since their central cylinder is protostelic. They resemble the two series mentioned, however, in being ventrisporangiate. The writer is of the opinion that the forking and arrangement of the fibrovascular strands in the blade of the leaf affords an unreliable criterion as to affinities, since if we considered the forking leaf trace rather than the relation of the foliar strands to the stele of the stem, it would be necessary to include certain Sigilliarieae with the Lycopsida in the sense of Dr. SCOTT and others with his Sphenopsida. A forking leaf trace and even a large leaf blade may occur in the lycopsid series, but neither of these is a palingenetic feature, as is clearly shown by the relation of the leaf trace to the central cylinder of the stem. There appears, in view of the considerations just described, no reason of sufficient weight for excluding the Equisetales, Psilotales, and Sphenophyllales from the phylum Lycopsida, since they possess all the essential characters of this great group. At best these three series can be aggregated only as a subgroup under the main heading Lycopsida.

NOTE.—It is a fact, apparently not without significance, that the various recent English writers, who are impelled to disagree with the present author's views as to the absence of foliar gaps in the Equisetales, have not made any reply to the seemingly unanswerable arguments in favor of these views, but have contented themselves with the mere reiteration of a dissentient opinion.

The conviction is continually repeated, in recent English publications bearing on this subject, that the gaps above the leaf traces in the modern Equisetales, but separated from their supposedly corresponding traces by the whole thickness of the so-called nodal wood, are in reality foliar gaps. An insuperable difficulty in this view, in addition to the very important anatomical ones cited by the present writer, is the fact that in both paleozoic and mesozoic representatives of the Equisetales the supposed foliar gaps are sometimes twice as numerous as the traces. It follows, of course, that some of the putative foliar gaps were not in reality leaf gaps in the older representatives of the Equisetales. This state of affairs, brought into strong prominence by recent Swedish investigations on mesozoic Equisetales, seems to furnish the necessary *coup de grace* to the views tenaciously held in England.

SUMMARY

1. The Pteropsida represent a great natural phylum of vascular plants characterized by dorsisporangiate sporophylls and by palingenetically large leaves, as inferred from their anatomical relations.

2. The pith of the Vasculares, in all cases where definite evidence is available, is an inclusion of the fundamental tissues of the cortex on the part of the stele.

3. The concentric type of tubular central cylinder is more ancient than the collateral and antedates the latter, as is shown by the persistence of the concentric condition in many leaf traces, where it has become obsolete in the stem.

4. So far as the primary bundle system of the Vasculares is concerned, they present a reduction series, in which the ferns and lower gymnosperms (Archigymnospermae) represent the earlier and more complex stages, and the higher gymnosperms (Metagymnospermae) and dicotyledons the phases which are more recent and more simplified.

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EXPLANATION OF PLATE XIII

FIG. 1.—Transverse section of the stem of *Onoclea Struthiopteris;* ×5.

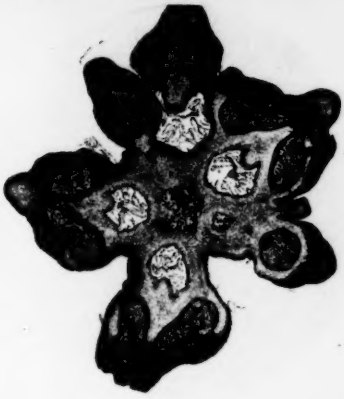
FIG. 2.—Transverse section of a part of the stem of the same species; ×10.

FIG. 3.—Transverse section of the base of the pinnular axis of *Angiopteris evecta;* ×10.

FIG. 4.—Transverse section of the same at a higher level, showing the fusion of the marginal bundles of the foliar system; ×10.

FIG. 5.—Transverse section of the rachis of *Marattia alata;* ×10.

FIG. 6.—The same, showing the exit of the vascular supply of a secondary axis; ×10.



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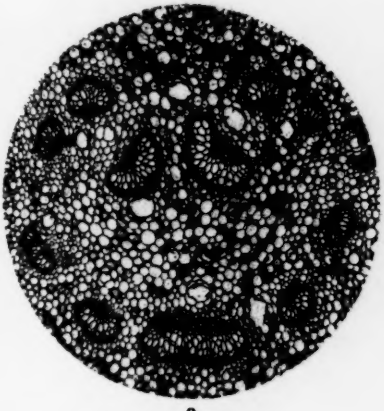

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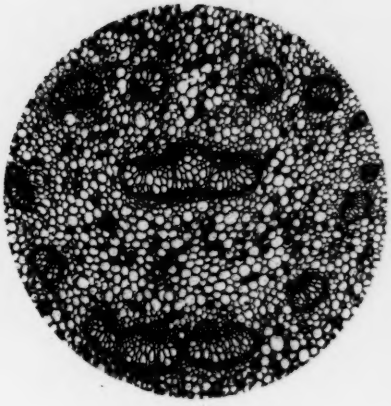

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JEFFREY on PTEROPSIDA

FERTILIZATION AND EMBRYOGENY IN DIOON EDULE[1]

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 141

CHARLES J. CHAMBERLAIN

(WITH PLATES XIV–XVII)

Fertilization in *Dioon edule* occurs from the second week in April to the second week in May. I have not been able to visit Mexico at this season of the year, but through the kindly influence of Gov. TEODORO A. DEHESA, who for several years has aided me in my investigation of Mexican cycads, and through the constant co-operation of Mr. ALEXANDER M. GAW, of the State Bureau of Information, Xalapa, Mexico, I have been able to secure material as regularly as if I had lived at Chavarrillo, where *Dioon edule* is most abundant. In cones picked at Chavarrillo, April 10, 1905, and examined at Chicago, April 21, nearly every nucellus contained one or more pollen tubes in which sperms were swimming vigorously; the next day there were not so many, and three days later nearly all pollen tubes had discharged their sperms; but as late as May 10 a few sperms were found. Consequently it would be possible for fertilization to occur at this late date, although not very probable, for all eggs capable of fertilization would probably have been fertilized already. A large cone picked at Chavarrillo, April 16, 1910, and examined at Chicago seven days later, contained embryos four times as long as the archegonia; consequently fertilization must have occurred as early as April 7. A few embryos in this cone were still in the free nuclear stage, but no pollen tubes were seen. These cones indicate the limits of the fertilization period as observed in the collections of six seasons. April 15 may be regarded as the optimum time, with fertilization frequent a week earlier and a week later, but becoming rare beyond these limits.

While fertilization may be somewhat delayed in cones sent to such a distance, the processes must be normal, for embryos

[1] Investigation prosecuted with the aid of a grant from the Botanical Society of America.

develop up to the cotyledon stage even in cones from which most of the sporophylls have been removed in securing material. In cones which arrive in Chicago with embryos in early cotyledon stages, the development is completed perfectly and the seeds will germinate.

Fertilization

The relations of the various structures at the time of fertilization are shown in fig. 1. The outer fleshy coat of the ovule has become highly differentiated, with its epidermal and hypodermal layers and deeper tissues containing tannin cells, mucilage ducts, and the outer vascular system. The stony coat has become so hard that it is difficult to cut it with a strong pocket knife; in fact, material of this and later stages was secured by sawing the ovule transversely with a fine saw. The inner fleshy coat has been reduced to a thin, papery membrane which, in the figure, appears as a dark border lining the inner surface of the stony layer. The nucellus, with its conspicuous beak and pollen tubes, has begun to sag. The tissue of the female gametophyte has become quite firm and contains numerous tannin cells, while the archegonial chamber has reached its maximum depth, and the nucleus of the central cell of the archegonium has just divided to form the ventral canal and egg nuclei. As stated in the paper on spermatogenesis in *Dioon edule* (**8**), the archegonial chamber is moist but contains no liquid before the pollen tubes begin to discharge. The sperms in escaping through the rather small rupture in the end of the pollen tube—there is no pit or pore—are much constricted, but soon regain their form and begin to swim. The amount of liquid discharged by a single pollen tube is small in comparison with the size of the archegonial chamber, and if the liquid should spread evenly, it would not be sufficient to cover the sperms; however, it behaves somewhat like a drop of water on a greasy surface, not spreading much, but moving until it comes into contact with the neck of an archegonium. The sperms move vigorously after being discharged from the pollen tube, but how long they might continue to swim under natural conditions in the archegonial chamber could not be determined. I had little success in keeping them alive in sugar solutions. When a sperm comes

into a sugar solution, the nucleus often slips out from the cytoplasmic sheath, and the cytoplasm then rinses off from the spiral band, leaving the band with its cilia almost free from any cytoplasm.

Before the pollen tubes have begun to discharge, the megaspore membrane over the archegonia has been ruptured, so that there is no obstruction between the sperms and the necks of the archegonia.

What causes the sperm to enter the egg? The classical experiments on chemotaxis would suggest a solution, but there is no free open passage as in bryophytes and pteridophytes, in which the small sperms may move freely in response to a slight stimulus. On the contrary the neck is closed, and the sperm becomes greatly constricted while entering, so that, whatever the force may be, it is a very strong one. Against the theory that chemotaxis is responsible for the movement, it must also be remembered that so skilful an investigator as MIYAKE (**5**) was unable to detect any chemotactic response when studying the sperms of *Cycas revoluta*, although he used the solutions which are uniformly effective with the sperms of pteridophytes, and in addition used the squeezed-out contents of the *Cycas* eggs.

It is well known that in many algae a small portion of the contents of the egg is extruded just before fertilization, a passage to the egg being facilitated in this way. In *Dioon*, just before fertilization, numerous preparations show a little protoplasm about the necks of the archegonia, and for a long time I assumed that it had been squeezed out from the egg by the pressure of the knife as the square block containing the archegonia was being cut out from the top of the endosperm before fixing. It was also noted that when material near the fertilization period is dropped into water or the fixing agent, a small bubble appears at the neck of the archegonium. The drop of liquid from the pollen tube has a very high osmotic pressure, and when it comes into contact with the extremely turgid neck cells, these lose so much of their contents that, in preparations, they appear more or less plasmolyzed. The pressure within the egg has been increasing until the contents are retained only by the rigidity of the turgid neck cells, and consequently even a slight decrease in turgidity of the neck cells would allow the escape of a small portion of the cytoplasm of the upper part of the egg, together,

probably, with some gas. In this way there is formed at the apex of the egg a vacuole, which may be of very short duration. In the absence of more definite knowledge, we suggest that this series of conditions would result in drawing the sperm into the egg, the cilia merely keeping it oriented, for sperms just within the egg showed the apex in advance in every case observed. It has already been noted in the paper on spermatogenesis (**8**) that the sperms have an amoeboid movement in addition to the movement by cilia. This amoeboid movement doubtless facilitates the entrance into the egg.

While the whole sperm enters the egg, the nucleus soon slips out from the cytoplasmic sheath and moves toward the egg nucleus, leaving the sheath with its ciliated band in the upper part of the egg. It may be that the constriction of the sperm during its entrance into the egg loosens the sheath from the nucleus so that it slips out more readily, for projections of various sizes extend from the nucleus into the sheath, and these would naturally become loosened. When more than one sperm enters the egg, it is worth noting that the nucleus of the second sperm does not slip out from the sheath, but remains intact in the cytoplasm at the top of the egg, where it may be distinguished to rather late stages in the development of the proembryo. Doubtless the first sperm opened the neck of the archegonium, so that the second suffered little constriction and the cytoplasmic sheath was not loosened. In some cases, at least, the sperm is still capable of vigorous movement after it is within the egg, as may be seen in fig. 1, where the contents of the egg have been stirred by the vibration of the cilia.

The cytoplasm of the sperm gradually mingles with that of the egg, and the two soon become indistinguishable, but the ciliated band maintains its identity much longer, and may be distinguished throughout the free nuclear development of the embryo, after which it becomes faint and finally merges with the cytoplasm of the upper part of the egg. As in *Zamia* (**4**), portions of the band occasionally penetrate farther, sometimes being found below the middle of the egg. The cytoplasm never surrounds the fusion nucleus, as in some gymnosperms, and there is no indication that it exerts any active influence upon the egg. That it does not stimulate is

evident from the fact that development is weakest in the upper portion of the egg.

The nucleus of the sperm enlarges somewhat during its passage to the egg nucleus, but details in the changes in its chromatin and changes in the chromatin of the egg nucleus were not studied. No preparation was secured which would show whether the chromatin contributions of the conjugating nuclei are distinct, as in *Pinus*, or whether the nuclei fuse in the resting condition, as is claimed for some gymnosperms. For a study of the nuclei at the time of fusion, *Ceratozamia* is a more favorable form, and consequently this feature will be investigated in that genus.

Embryogeny

HISTORICAL

The development of the cycad embryo has been studied in only two genera, *Cycas* and *Zamia*, and a few rather later stages have been noted in *Ceratozamia* and *Encephalartos*.

As early as 1877 WARMING (1) described some of the later stages in the development of the embryo of *Ceratozamia*, but in all cases the embryo had already passed through the base of the egg and invaded the endosperm. He noted the long suspensor and particularly the single cotyledon, a feature which Sister HELEN ANGELA (6) has since proved to be due to gravity, the missing cotyledon always appearing when developing seeds are rotated on a klinostat.

TREUB'S account of *Cycas circinalis* (2) in 1884 was comparatively full. A prolonged period of free nuclear division results in the formation of numerous free nuclei which are crowded to the periphery by a large central vacuole. Wall-formation then begins and the embryo, with its long suspensor, is organized from the cells at the base of the proembryo.

IKENO'S (3) account of *Cycas revoluta* confirms TREUB'S except in regard to the formation of the vacuole. IKENO finds that a large number of small vacuoles appear in the cytoplasm of the central portion of the egg, and that this central portion with its contained nuclei then disorganizes, leaving a parietal layer of protoplasm and nuclei, while a single large vacuole occupies the

center. After this stage, there are a few free nuclear divisions at the base of the egg before walls begin to appear, and at the same time amitotic divisions may take place in the upper portion.

COULTER and CHAMBERLAIN (4) found in *Zamia floridana* a somewhat different condition. After about eight simultaneous free nuclear divisions, giving rise to 256 free nuclei, walls appear at the base of the proembryo, just as in the formation of endosperm in most angiosperms, but no vacuole is developed.

SAXTON (9) has recently described some of the later stages in the embryo of *Encephalartos*. He finds that the suspensor is a root cap, and that the embryogeny is very similar to that of *Ginkgo*.

DIOON; FREE NUCLEAR PERIOD

In *Dioon edule* fertilization is followed immediately by a long period of simultaneous, free nuclear division. The first mitosis of the fusion nucleus occurs in the position where fertilization has taken place, a little above the middle of the egg, the spindle being oblique, as is usually the case in gymnosperms. The succeeding mitoses follow rapidly, and the nuclei, even as early as the 16-nucleate stage, become rather evenly distributed throughout the entire proembryo. Occasionally the nuclei move toward the bottom of the proembryo, the 16, 32, and 64-nucleate stages having been found with all the nuclei below the middle of the proembryo, and in one case a 64-nucleate stage had all the nuclei in the lower third. On the other hand, two 4-nucleate stages were observed with all the nuclei above the middle of the proembryo.

In stages following the 64-nucleate stage—resulting from the sixth mitosis—the number of nuclei in the lower part of the proembryo is likely to be considerably larger than that in the upper part. At the 128 and 256-nucleate stages—resulting from the seventh and eighth mitoses—the larger number at the bottom is due to a settling of the nuclei; but at the ninth mitosis some of the nuclei in the upper half of the proembryo may fail to divide, and thus add to the disproportion. It may happen, occasionally, that the ninth mitosis, which gives rise to the 512-nucleate stage, may be the last of the simultaneous divisions; but usually there is a tenth mitosis, which would give rise to 1024 nuclei, if all nuclei

should divide at every simultaneous mitosis. A rough estimate, based upon fig. 6, shows that the evanescent walls, to be described later, are those resulting from the tenth mitosis; and fig. 7, in which permanent walls have been established, shows that in this proembryo the permanent walls appeared in connection with the tenth mitosis. We have not found any case which would indicate an eleventh mitosis, and only a few cases where permanent walls seem to have been formed at the ninth mitosis; while nearly all proembryos in approximately the stage shown in fig. 7 indicate that there have been ten mitoses with permanent walls beginning in connection with the tenth.

During the period of free nuclear division, the figures are entirely intranuclear and are characterized by the abundance and persistence of the spindle fibers (figs. 2–4). The nuclear membrane is formed quite late (fig. 3), but when once formed it becomes unusually thick, and pieces of it may be seen until late prophase or early metaphase of the next mitosis (fig. 2, *n*).

DIOON; EVANESCENT SEGMENTATION

The most characteristic feature of the proembryo of *Dioon edule* is the complete but evanescent segmentation of the entire egg. In one case, as early as the 64-nucleate stage, faint walls were observed dividing the entire proembryo into uninucleate cells. Such walls break down completely before the next mitosis begins. At the seventh and eighth mitoses, giving rise to the 128 and 256-nucleate stages, the appearance of walls is more frequent and they break down less rapidly; while at the ninth mitosis, giving rise to the 512-nucleate stage, the walls are probably always formed; and at the tenth division the walls are formed; but while they disappear in the upper portion of the proembryo, leaving it in free nuclear condition, they persist at the base, constituting the first permanent walls. As soon as the proembryo becomes cellular, the simultaneous mitoses are succeeded by the scattered mitoses which one expects in a young cellular embryo.

The evanescent walls consist of broad bands of spindle fibers, about two-fifths of the spindle nearest the daughter nuclei disappearing very early, while the middle fifth remains long enough to

cause a segmentation which is so conspicuous that it is seen easily with a pocket lens (figs. 5, 6).

The evanescent walls were, for a time, the most puzzling feature in the embryogeny, especially while it was thought that they belonged exclusively to some particular mitosis. As observations multiplied and it became evident that the evanescent segmentation might occur at the sixth mitosis and was increasingly frequent at the seventh, eighth, and ninth mitoses, the explanation became evident. The early mitoses, up to the sixth, follow in such rapid succession that a new mitosis is begun before the preceding one could establish a wall. Between the succeeding mitoses the intervals are increasingly greater, and consequently the natural tendency of a spindle to develop a wall finds a more marked expression.

We regard the appearance of evanescent walls as a reversion, indicating that the ancestors of *Dioon* had embryos which were cellular throughout. It can hardly be questioned that the free nuclear condition in gymnosperms, whether in the proembryo or in the gametophyte, is not a primitive but rather a highly specialized condition. In the small eggs of the pteridophytes, including even the heterosporous genera, the first nuclear division is followed by the formation of a wall. We suggest that free nuclear division in the proembryo of gymnosperms arose in connection with the increasing size of the egg, the increased mass of the egg becoming too large to be segmented, and at the same time the large mass favoring rapidly succeeding mitoses. The nuclei divide simultaneously because exposed to practically similar conditions. As mitosis continues and the mass of cytoplasm about each nucleus becomes less, the mitoses succeed each other less rapidly, and as the relation between the nuclei and surrounding cytoplasm approaches that which is found in the ordinary tissues, segmentation begins. If this view is correct, we should expect the most extensive free nuclear periods in the largest eggs, and such is certainly the case. The egg of *Dioon edule* often reaches a length of 5 mm., and the number of free nuclei is about 1000, theoretically 1024. *Zamia*, with an egg about 3 mm. in length, has 256 free nuclei; and *Gingko*, with an egg of somewhat approximately the

same mass, shows the same number. The much smaller eggs of Coniferales have comparatively short free nuclear periods, showing only 32, 16, 8, 4, and 2 free nuclei; while in the small egg of *Sequoia* the first mitosis is followed by a wall.

While it might be tempting to regard this as a reduction series, and to regard forms with a large number of free nuclei as primitive, it seems probable that the number of free nuclei is correlated merely with the size of the egg. That the large number does not prove antiquity is shown by the fact that *Dioon* has 1000 free nuclei, while *Pinus* has only 8 (i.e., walls appear in connection with the 8-nucleate stage), and yet *Pinus* is much more ancient than *Dioon*. We should expect to find the critical forms among the lower Cycadofilicales as they began to be differentiated from some heterosporous fern ancestry. These forms, which are still to be discovered, should have small eggs with complete segmentation not preceded by any free nuclear period, the free nuclear feature appearing later in connection with an increased size of the egg. Although this is highly theoretical, we believe that it suggests an explanation of the structures as we find them in living gymnosperms.

DIOON; THE CELLULAR EMBRYO

At the last mitosis of the free nuclear or evanescent segmentation period, permanent walls are developed at the base of the proembryo, the walls in the upper part being evanescent and disappearing as before. The nuclei in this upper region do not divide any more and many of them disorganize. In the basal region nuclear division, always accompanied by cell division, progresses rapidly; and while one can still estimate with some degree of exactness the extent to which the free nuclear stage has progressed, a small-celled tissue is formed (fig. 7). At the stage shown in this figure, there is practically no indication of regions corresponding to the "rosette," suspensor, and embryo proper regions of many conifers. At this stage the archegonium jacket is still conspicuous, and at the base of the proembryo the jacket has become extended into a tissue several cells deep, contrasting sharply with the adjacent starchy cells of the endosperm. Cellulose walls have formed on the peripheral surfaces of the cells of this proembryo and the egg membrane is still intact.

Very soon after the stage shown in fig. 7, a differentiation becomes apparent. A thick wall forms a sort of diaphragm between the definitely cellular and the free nuclear or loosely cellular portions of the proembryo (figs. 8, 9, *d*). Just below the diaphragm the cells are large and with scanty protoplasmic contents, while one and in the middle two layers of cells are much smaller and have dense protoplasmic contents (fig. 8). This more deeply staining region at the tip becomes the embryo proper, while the large cells, in contact with the diaphragm, will differentiate into the suspensor. Long cells like *a* and *b* in fig. 8 may divide again, the outer cell then contributing to the suspensor, while the other forms a part of the "rosette" and never gets beyond the original limits of the egg. The suspensor cells now divide both longitudinally and transversely, and it becomes difficult or impossible to distinguish any boundary between suspensor and embryo proper (fig. 9). As the periclines at the tip of this figure indicate, the dermatogen has not yet been differentiated. In both figs. 8 and 9 the embryos have not yet pierced the egg membrane.

The egg membrane now disorganizes, apparently becoming digested, and the rapidly elongating suspensor thrusts the embryo through the base of the egg into the endosperm. At this time mucilage ducts begin to appear in the suspensor (fig. 10). As soon as the embryos break through the egg membranes, the four or five or six suspensors become twisted together, and as one dissects them out they appear like a single suspensor with one embryo at the tip; but when they have reached a length of 1 cm., a careful examination with a pocket lens will show unsuccessful embryos at various distances from the egg region and a single embryo at the tip. I have never seen a suspensor branching, as described for *Encephalartos* by SAXTON (**9**), but have seen unsuccessful embryos which project somewhat from the general suspensor and so caused the appearance of branching.

The suspensor is a remarkable feature of the cycad embryo. Its growth and twisting is accompanied by an extensive disorganization of the endosperm in the archegonial region, especially just beneath the archegonia, so that there is formed a large cavity which becomes filled with the long suspensor. The cavity is moist,

but not full of liquid. The cells disorganized in the formation of the cavity must have contributed largely to the growth of the suspensor, since the embryo itself is receiving from surrounding cells enough to account for any increase in its size. That the suspensor exerts a vigorous thrust is evident from the fact that when released it relaxes like a spring which has been under tension. The suspensor when stretched out reaches a length of 75 mm. As the embryo matures, the suspensor does not disorganize, but remains as a tough dry thread, strong enough to lift the weight of the entire embryo.

The embryo develops rapidly, cell division taking place throughout the entire embryo, while the suspensor cells elongate and also occasionally undergo mitosis (figs. 10–12). In the last figure the two upper mitoses are in the suspensor and the three lower in the embryo proper. It is interesting to note that such mitoses are found in cones which have been taken from the plant in southern Mexico, shipped to Chicago in a basket, and after arriving have been lying on the laboratory table for two or three weeks.

The first indication of any differentiation of the embryo proper is the appearance of increased vigor in cell division in the region just below the suspensor, indicated by *x* in fig. 14. This region, which appears in the embryo and not in the suspensor, is the beginning of the coleorhiza, an organ which rapidly becomes conspicuous and soon constitutes the largest part of the embryo (figs. 15, 16).

While the coleorhiza and the root cap are spoken of as two organs, and while they differ widely in general appearance, in cell structure and in function they are morphologically only one organ, the root cap. The coleorhiza at first consists of thin-walled cells with numerous large starch grains, but toward the close of the intraseminal period the cell walls become very hard and thick, so that the term coleorhiza is quite appropriate. Just within the coleorhiza the mature embryo shows a cone of thin-walled cells, rich in tannin, derived from the same meristem, the beginning of which is seen in fig. 14. These cells are the outer layers of the root cap. At germination the pressure is developed, at least in large part, by the activity of the meristem which is adding new

layers to the root cap. The pressure, crowding the coleorhiza against the micropylar end of the seed, causes an irregular jagged fracture of the stony coat of the seed, through which the embryo emerges. It is only after the fracture is large enough to permit the exit of the embryo that the root cap pierces the central portion of the coleorhiza, the thick-walled cells of which may be seen clinging to the root in threadlike masses even after the axis of the seedling has become vertical.

The late differentiation of body regions is a noticeable feature of the cycad embryo. At the stage shown in fig. 15, not only is the differentiation into periblem and plerome still incomplete, but even the dermatogen is not yet differentiated, as may be seen by the periclines in the cotyledons and especially in the stem tip (figs. 15, 17). Perhaps the importance of division by anticlines only has been overestimated, for in this embryo the outer layer looks like a dermatogen long before the periclines cease to appear.

A general view of an embryo at the stage shown in fig. 15 may be seen in the accompanying diagram (fig. 16), drawn from the same preparation. Just below the suspensor with its large mucilage cavities is the swollen coleorhiza. Starch is found in the suspensor, but is most abundant in the peripheral and lower regions of the coleorhiza. Cell division is most active in the dotted region of the stem tip. While the general appearance of the mitoses is very different from that described for the free nuclear period, it is probable that the difference is not so great as it seems, for in fig. 18 the spindle may mark the limit of the nuclear membrane.

A diagrammatic section through a ripe seed is shown in fig. 19. The embryo extends almost the entire length of the seed, the cotyledons constituting the principal mass. The first functional leaf, if drawn on a large scale, would show the primordia of pinnules, the scale leaves not showing such a differentiation. The outer fleshy layer and the middle or stony layer (shaded) are easily distinguished, but the inner fleshy layer, while forming a conspicuous membrane containing the inner vascular system, is too thin to be shown in the diagram. Although the stony layer is quite thin in the region of the pit at the base of the seed, the cotyledons never emerge at

that point, but remain in the seed, sometimes until the seedling is three or four years old.

The embryo may develop continuously, germinating without any resting period, or may germinate after a resting period. Seeds which had been in the laboratory for two years germinated readily, but how long they might retain their power of germination is uncertain.

While the general course of development in the later stages of the embryo is the same in all of my material (*Dioon*, *Ceratozamia*, *Zamia*, *Microcycas*, and *Encephalartos*), there are considerable differences in details which may prove suggestive, and consequently no more detailed description will be given until a comparative study has been made.

The development of the vascular system of the embryo and seedling of *Dioon edule* has been investigated in this laboratory by THIESSEN (**7**).

Summary

1. The liquid from the pollen tube causes a decrease in the turgidity of the neck cells, and this allows a portion of the upper part of the egg to escape, thus forming a vacuole at the top of the egg. The entire sperm is thus drawn into the egg.

2. There are sometimes nine, but oftener ten simultaneous free nuclear divisions, resulting in the formation of 512 or 1024 free nuclei.

3. There is a complete but evanescent segmentation of the entire proembryo, the walls then disappearing except at the base of the proembryo, where they become permanent.

4. The coleorhiza and root cap, although differing in appearance, cell structure, and in function, are formed from the same meristem, and both are morphologically root cap.

5. Plerome, periblem, and dermatogen are differentiated quite late in the development of the embryo.

6. The seed germinates without any resting period, but also has been germinated after a rest of two years.

THE UNIVERSITY OF CHICAGO

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DESCRIPTION OF PLATES XIV–XVII

FIG. 1.—Upper part of ovule at the time of fertilization; the figure is reconstructed from several sections; the pollen tube on the left shows the body cell still undivided; the one in the middle shows two sperms and the remains of the stalk and prothallial cells; next to this tube is one in which the body cell has just divided, and the prothallial and stalk cells are still turgid; two pollen tubes which have discharged their contents are also shown; the dark line below the outer part of the nucellus is the megaspore membrane.

FIG. 2.—Late prophase during the free nuclear division in the proembryo, showing the intranuclear membrane (*n*). ×480.

FIG. 3.—Early telophase during the free nuclear period; the nuclear membrane has not yet been formed. ×480.

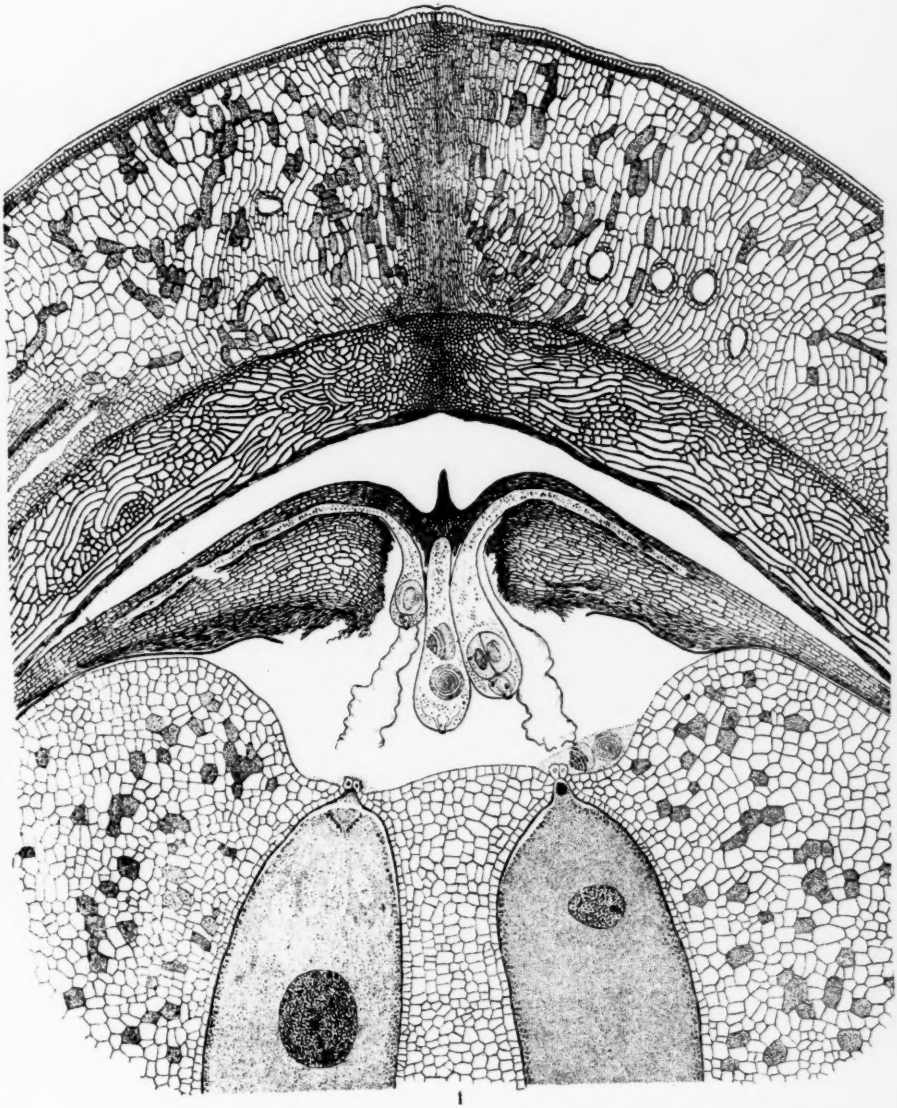
FIG. 4.—Telophase during free nuclear period; the central portion of the fibers from the evanescent walls. ×480.

FIG. 5.—Lower part of proembryo, showing evanescent but complete segmentation.

FIG. 6.—Diagram showing the complete proembryo of which fig. 5 shows only the lower part.

FIG. 7.—Lower part of proembryo, showing permanent walls at the base.

FIG. 8.—Young embryo: *d,* diaphragm; *f,* free nuclei; *a* and *b,* cells which may contribute to both "rosette" and suspensor.



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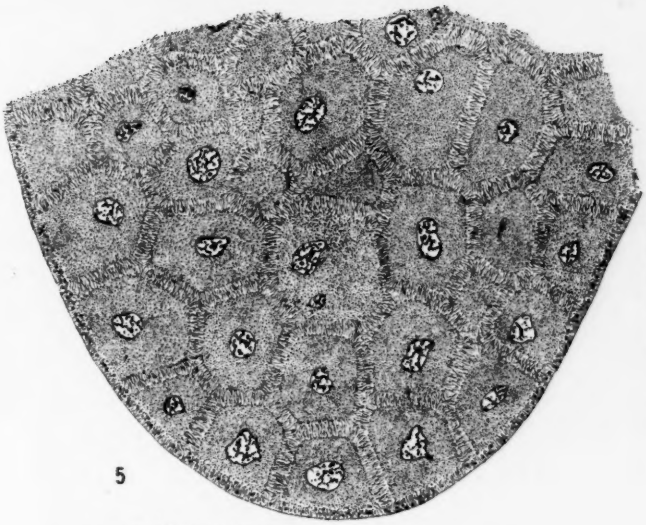

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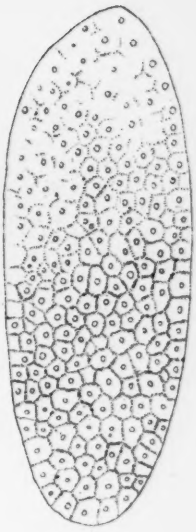

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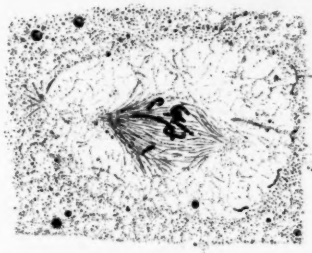

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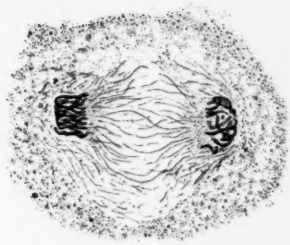

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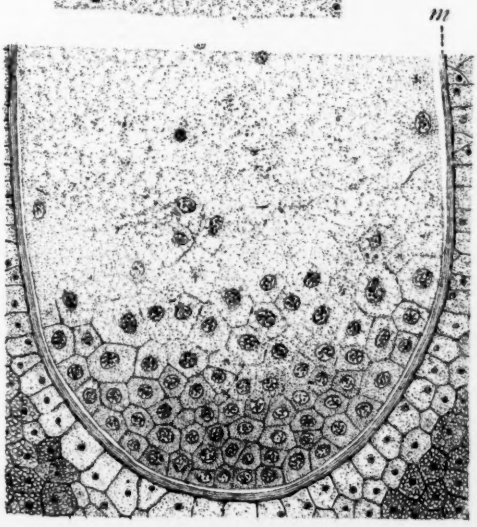

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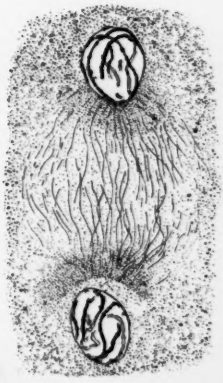

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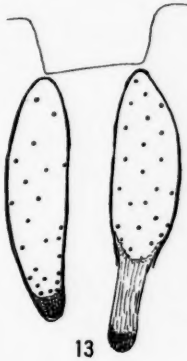

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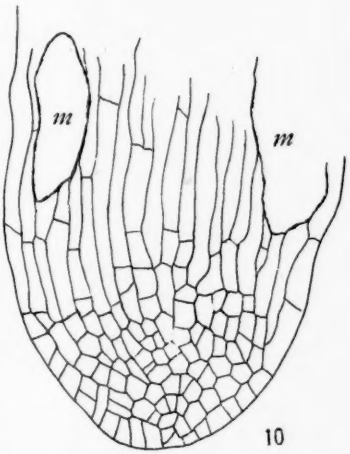

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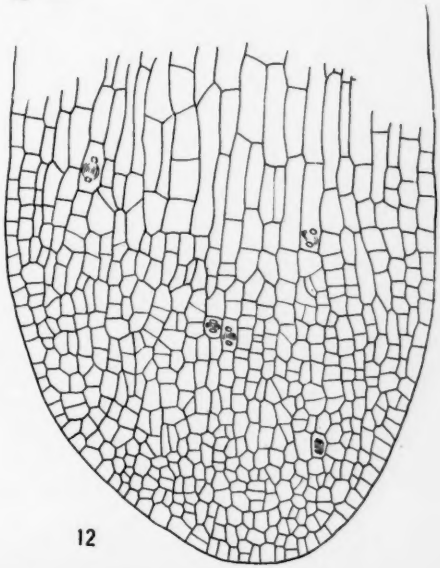

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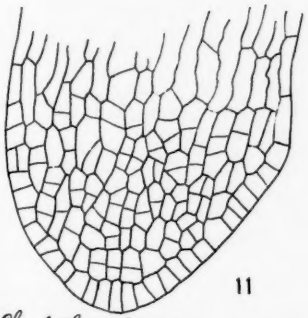

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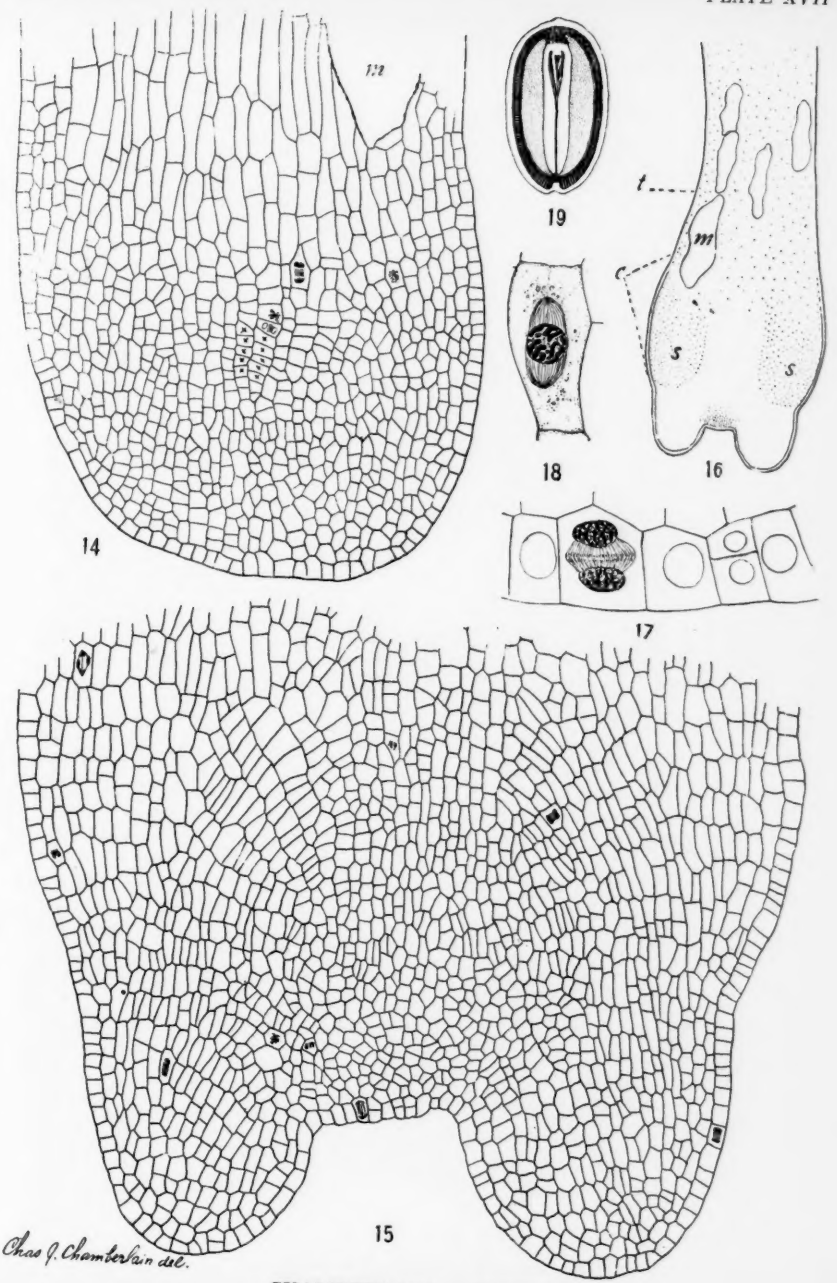
Chas. J. Chamberlain del.

CHAMBERLAIN on DIOON



CHAMBERLAIN on DIOON

FIG. 9.—Later stage, just before the embryo breaks through the base of the egg; the proembryo at the left in fig. 13 is in this stage.

FIG. 10.—Embryo after the suspensor has begun to elongate: *m*, mucilage cavities; the proembryo at the right in fig. 13 is in this stage.

FIG. 11.—A somewhat later stage.

FIG. 12.—Embryo shortly before the differentiation of cotyledons.

FIG. 13.—Diagram showing the topography of embryos at the stages shown in figs. 8–12.

FIG. 14.—Embryo showing the beginning of the meristem which is to produce the coleorhiza and later the root cap: *x*, the meristem; *m*, mucilage cavity in the suspensor.

FIG. 15.—Early cotyledon stage; the broader portion back of the cotyledons is coleorhiza; the periclines show that the dermatogen is not yet differentiated.

FIG. 16.—Diagram of the stage shown in fig. 15: *t*, suspensor; *c*, coleorhiza; *m*, mucilage cavity; the cells of the dotted region (*s*) are rich in starch; the cells of the dotted region at the stem tip are small, but slightly vacuolate and contain numerous figures.

FIG. 17.—Portion of the outer layer at the stage shown in fig. 16, showing that periclines are still taking place and that consequently the dermatogen is not yet differentiated.

FIG. 18.—Mitotic figure in the suspensor, showing rounded poles of the spindle.

FIG. 19.—Ripe seed, showing embryo with long cotyledons, the first leaf at the left, a scale leaf at the right, the coleorhiza (shaded), the stony layer (shaded), the outer fleshy layer, and the inner fleshy layer represented only by a fine line.

NOTES ON CHILEAN FUNGI. I

CONTRIBUTIONS FROM THE CRYPTOGAMIC LABORATORY OF HARVARD UNIVERSITY, LXVI

ROLAND THAXTER

(WITH PLATES XVIII AND XIX AND ONE FIGURE)

During the months of February and March 1906, it was my good fortune to pass six weeks of the antarctic summer and early autumn in the town of Punta Arenas, on the Straits of Magellan. These months being in many respects the most favorable for botanizing in this cold and wind-swept region, I had an excellent opportunity to become acquainted with its fungus flora, which was much richer and more varied than might have been expected, in view of the comparatively scanty phanerogamic flora and the general severity of the climate. Although for about a week in late February the mercury rose above 60° F. every day, and once even reached 70°, the mean diurnal temperature during the remainder of my stay was below 60°. Freezing temperatures were not uncommon, and it was not unusual in the morning to see the green beech forest on the hills to the west of the town loaded with snow. The small pools, in the localities where I collected, were often frozen over as late as the middle of the forenoon, while icicles might be seen hanging from flowers and grass growing on the dripping south slopes of the ravine which led to my usual collecting ground.

The town of Punta Arenas is not favorably situated as a base from which to make botanical excursions, since the whole shore of the Strait, as far as one can see to the south and for many miles to the north, has been devastated by fire; and the general aspect presented to the newcomer, as his steamer drops anchor in the open roadstead opposite the town, is to the last degree unattractive and forbidding. Formerly a superb forest of the antarctic beech (*Nothofagus*) covered the whole region, extending from the water's edge over a somewhat undulating plain, which gradually rises to the base of a range of hills or low mountains, the highest not

2000 feet above the sea, which form a wooded background for what is now a ghastly waste of dead trees still standing or fallen in confused heaps; and forming in many places, as one approaches the limits of the living forest, an almost impenetrable barrier.

Nearer the shore the dead trees have been largely cleared away, and the forest has given place to a firm turf which has taken possession in the vicinity of the town, and is grazed by divers domestic quadrupeds, so that there is no chance for reforestation. Over this area are scattered stunted specimens of the so-called varieties *bicrenata* and *uliginosa* of *Nothofagus antarctica*, some larger trees of the latter persisting in thin groves near the shore; while everywhere are clumps of "califate" bushes (*Berberis buxifolia*), associated with a flora of low annuals and perennials, which, though not very varied as to species and genera, is yet of the greatest interest to one unacquainted with its features.

The fungi occurring in connection with this coastal region are, like the flowering plants, for the most part different from those of the beech forest, and are more numerous than might have been expected, including a variety of striking forms. Among these the hexenbesen of the superb *Aecidium magellanicum*, to which it is my purpose to refer in a future note, are everywhere conspicuous on the califate, which harbors also several other rusts. Familiar forms are not altogether wanting, and *Psalliota campestris* grows in profusion over the turfy area, as well as a large puff ball which I took to be *Lycoperdon coelatum*. *Coprinus comatus* and *C. atramentarius*, entirely typical in appearance, were also occasionally seen about the town, and all of these formed a most welcome addition to the canned diet which prevails in these latitudes.

In order to reach the living forest where most of my collecting was done, it was necessary to traverse the coastal region above described: and this is most readily accomplished by following a narrow-gauge railroad which skirts the bed of the Rio de las Minas, traversing a portion of the deep gorge cut through the hills by this small stream, which, flowing from the west, empties into the Strait, after passing through the northern portion of the town. Even this broad ravine, which one enters somewhat abruptly after a tiresome walk of several miles against the biting wind which blows

almost without cessation from the west, has not been spared by fire, and its steep banks were capped by a skeleton forest; on the north more recently burned than elsewhere and carpeted for miles with fruiting *Marchantia*. It is thus not till one has passed the small coal mine from which the stream takes its name, and which forms the objective point of the railroad, that, after a walk of six or seven miles from the town, he finds himself in the living forest. Even here destruction of another kind was steadily progressing during my visit, and the lumberman's axe was rendering worse confounded the confusion already existing in the tangle of fallen trunks which seems to be characteristic of these woods.

When one considers that the trees composing this forest in the immediate vicinity of my collecting ground belong to only two species of a single genus, the variety of fungi which inhabit it is unexpectedly great. That a heavy forest of often very large trees should develop under such climatic conditions as have been described, is surprising; but that beneath its shade a considerable flora of the more fragile and perishable forms of fungi should develop, is even more difficult to understand. Yet here are found Amanitas, and other softer agarics, among which a very fine and large *Coprinus* is conspicuous, growing in masses from beneath fallen logs; Hymenogastreae are common and other soft hypogaeous forms, as well as Pezizae, Myxomycetes, etc., all flourishing and maturing in this valley; where, though the surrounding hills afford some shelter, the mercury can seldom rise much above 60° F., while freezing temperatures are common at night even in midsummer, with frequent cold squalls of rain, hail, or snow. Although I made no special effort to collect them, I gathered about forty species of Myxomycetes, and I have never seen Hymenogastreae more abundant, in numbers of individuals at least. The more resistant forms of fungi were duly represented, especially the Pyrenomycetes; although the Polyporei, as elsewhere in the Chilean forests, were scanty, and here in bad condition. Of all these fungi, however, the most peculiar was the discomycetous *Cyttaria*, and the nearly spherical distortions of the esculent *C. Darwinii*, often reaching a diameter of several feet, were everywhere conspicuous on the trunks and branches, although I was too late to see in the

best condition the curious fructifications which sometimes hung by dozens from their under sides.

It had just rained heavily as I stepped into these dripping woods, and I shall not soon forget the first day that I passed in them amid almost a surfeit of new botanical sensations. Not only were the fungi for the most part entirely new to me, but the trees were covered with unfamiliar lichens. One small filmy fern was common; but, in marked contrast to the forests farther north, hepatics were not abundant or conspicuous, with a very few exceptions like *Lepidolaena magellanica*, which covered fallen logs in many places. Mosses were abundant, especially along the ravine, and in the woods about the mine I found the lovely *Dissodon mirabile* Cardot, growing in tufts on cow dung, often in company with *Tayloria Dubyi* Broth., and conspicuous from its large pearly-white hypophyses.

Apart from the rather meager gatherings brought back by the various expeditions which have visited the Magellan region, our knowledge of its fungi is largely due to the fruitful investigations of Professor CARLOS SPEGAZZINI, an active collector and keen observer, whose published papers on the fungus flora of Tierra del Fuego and southern Patagonia bear witness to the varied character of this flora even in a portion of the forest much farther south; and this, too, notwithstanding the fact that a large portion of his collections were lost by shipwreck. During my stay on the Straits, although my collecting grounds were very limited and the forest so difficult of access, I was able to recognize a considerable number of the forms described by SPEGAZZINI, as well as certain others not included in his enumeration, or referred to, as far as I have been able to ascertain, in the works of other students of antarctic fungi; and it is the object of the present note to give some account of several of the latter, which were among the first that I met with in these fascinating woods.

On returning along the Rio de las Minas from my first excursion to the beech forest, I noticed on many of the smaller trees of *Nothofagus bicrenata* which covered the lower slopes of the ravine, especially on those which, from constant cropping by cattle, had assumed a bushy habit, but occasionally, also, on the lower

branches of larger trees, certain leaves, sometimes one or two together, but more often all the leaves of a twig or small branch, which were peculiar in appearance. These leaves were conspicuous from their paler yellowish-green color, which contrasted with the deep green of the healthy leaves, and were thicker and often distinctly larger than those of the normal foliage, as indicated in the accompanying text figure, photographed from dried material. Although every leaf of such twigs or branches was invariably affected, the latter showed little if any modification or distortion, and little if any tendency was observable to the formation of a witches broom, through the growth of adventitious shoots. The under side of these leaves were livid white in color, owing evidently to a continuous covering of asci, and I was greatly pleased to know that I had added a *Taphrina* to my overflowing basket of treasures.

On examining sections of this material, the asci proved to be rather stout, distally truncate or rounded, seated on a broader basal cell between the ruptured cutis and the epidermis, the outline of which was unbroken by any rhizoidal intrusion of the fungus between its cells. The asci were so densely filled with a very uniform coarsely granular fatty protoplasm, that no structures resembling spores were at first observed, and the material was laid aside on the assumption that it was immature. On reexamining it, however, and breaking the asci by crushing them, the coarse protoplasm was forced out, and I was astonished to see mingled with it great numbers of peculiar appendiculate bodies (fig. 6), so unlike any described ascospores of this group that it was not till I had actually seen them emerge from within the ascus when under pressure, that I was convinced of their true nature. After remaining in glycerin for some days, the granular contents of the ascus become modified, so that the spores, in different stages of development, are clearly visible (figs. 3, 4), and the origin of this singular habit in the mature spore is readily made out by a comparison of these stages (figs. 5, 6). The primary spores are always eight in number, relatively small in proportion to the size of the ascus (fig. 3), regularly oval in outline, and very uniform in size. As their development progresses, a bud appears at either extremity, which enlarges to form a stout, nearly cylindrical or somewhat

clavate, terminal appendage very constant in its form and dimensions, the axis of which coincides with that of the primary spore, and usually exceeds it in length. While these terminal appendages are developing, subterminal buds begin to appear about the base of each, normally four in number, less often two or three, which form a whorl of threadlike, divergent, slightly tapering appendages, rigid, straight or usually somewhat curved, and two to three times as long as the terminal ones. The origin of these subterminal

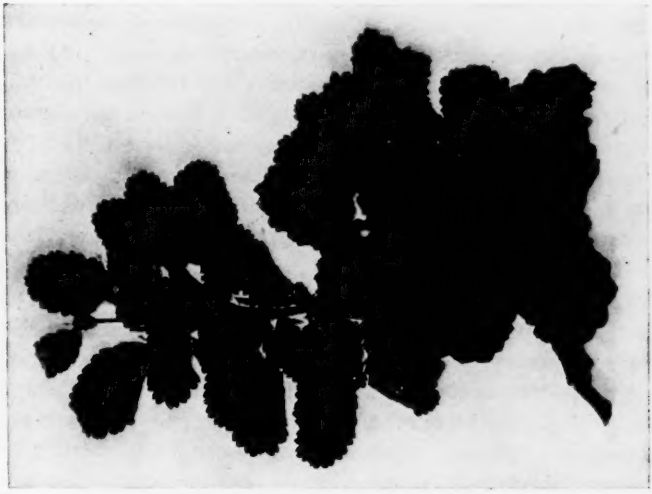


FIG. 1.—Branchlet of *Nothofagus antarctica* var. *bicrenata*, showing natural foliage at the left; the leaves at the right all attacked by the *Taphrina* and distinctly hypertrophied; slightly reduced from dried material.

appendages is often distinguished at maturity by a slight swelling, more or less clearly visible between the body of the primary spore and the base of the terminal appendage. As a result of the formation of these appendages, the primary spore is left nearly empty and is usually seen to be traversed by a single strand of protoplasm, while the terminal appendages, as they mature, become filled with dense refractive contents. These terminal appendages, moreover, evidently become the functional spores, since they readily separate from the empty primary spore, carrying with them the whorl of

threadlike subterminal appendages, which may perhaps be assumed to aid in their dissemination and lodgment after discharge. In crushed specimens these appendiculate terminal buds predominate, entire spores being comparatively infrequent.

That these extraordinary spores owe their peculiar structure at maturity to a specialization of the phenomenon which occurs in so many species of *Taphrina*, and which, through the budding of the primary spore, fills the ascus with yeastlike elements, seems highly probable; yet it is very remarkable that a phenomenon which, in other instances, is wholly indeterminate in character, the yeastlike elements being produced without regularity as to number, association, or differentiation as to function, should, in the present instance, be replaced by such a definite association of buds, which not only differ from one another in form and function, but are constant in number as far as the terminal buds are concerned, and at least subconstant as regards the subterminal ones. No further development nor any indication of germination in the primary buds was seen in any of the material examined.

The relation of the parasite to its host is a matter concerning which I have been unable to satisfy myself. In none of the sections examined, which were made from dried material, have I been able to detect any signs of fungus filaments penetrating the leaf or stem tissues, or extending themselves in any position except between the cutis and the epidermis. Nevertheless, the fact that all the adjacent leaves in branchlets of considerable size are completely involved, would point to the perennial nature of the disease, which may be presumed to extend from a hibernated mycelium in the young shoots to the unfolding leaves.

This species was subsequently found in abundance, not only along the ravine above mentioned, but on the larger trees of the forest, especially on the lower branches of such as grew along the margins of the open swampy glades characteristic of the region where I collected. It was also found less abundantly in the coastal region, not only on *Nothofagus antarctica* var. *bicrenata*, but also on the so-called var. *uliginosa*, a tree quite different in habit, leaves, and fruit, and growing in scattered colonies, especially to the south of the town of Punta Arenas. I may mention, in regard to these

hosts, that Professor SARGENT informs me that the determinations above given are confirmed by HEMSLEY, who suggests that the var. *uliginosa* should be considered a distinct species.

I saw no other species of *Taphrina* during my stay at Punta Arenas, nor did I find indigenous species elsewhere in Chile. About Santiago and in the central valley, where the Lombardy poplar is extensively planted, attaining a great size and forming one of the most conspicuous features of the landscape, the brilliant *T. aurea* was common, attacking the leaves of this host. *T. Ulmi* was also abundant on an introduced species of *Ulmus* planted about the Baños de Apoquindo, near Santiago; and throughout this whole region of the central valley the familiar *T. deformans* is destructive to the peach.

The *Taphrina* on *Nothofagus*, to which I have given a name suggested by the peculiarities of its spores, may be characterized as follows:

Taphrina entomospora, nov. sp.—Stratum ascorum livide-albidum, totam paginem inferiorem folii occupans, mycelio inter cuticulam et epidermidem nascente ortum: ascis dense confertis, subcylindricis, apice rotundatis vel subtruncatis, cellula basali latiore instructis; supra epidermidem positis: sporidiis entomomorphis, octonis, plasmate dense granuloso obscuratis; primum simplicibus, ovalibus; deinde appendiculatis, appendicibus biformibus; alteris utrinque terminalibus, rectis, cylindraceis vel subclavatis; alteris subterminalibus, saepissime quaternis, rigidis, tenuibus, divergentibus, subcurvatis, subattenuatis, utrinque cyclo oriundis: ascis 55—60×13—15 μ. Sporidiis 9—10×3—4 μ. Appendicibus terminalibus 8—12×3.5 μ, subterminalibus 15—25×0.8 μ.

In foliis vivis lutescentibus *Nothofagi antarcticae* var. *bicrenatae* et var. *uliginosae*. Punta Arenas, Magellanes, Chile.

My first day's foray yielded another remarkable fungus, associated with the *Taphrina* just described. While gathering material of the latter, I noticed that in some instances the leaves were covered by a glistening powder, and further examination showed that when the *Taphrina* occurred on twigs growing protected among the dense branches of small bushy trees, the powder was associated with reddish-brown perithecia evidently belonging to one of the Ery-

sipheae. This secondary parasite proved also not uncommon when sought for; but seldom fruited unless somewhat protected as above described. In one instance it was found spreading copiously from a twig affected by the *Taphrina* to the healthy foliage of the host; but in all other cases observed it was practically confined to leaves already affected by the other parasite. The perithecia being small and inconspicuous when scattered on the healthy leaves, it is not impossible that I may have overlooked it, and that it may naturally grow apart from the *Taphrina*. The reaction between the two, however, was very evident, the growth upon leaves invaded by the *Taphrina* being very much more luxuriant and the perithecia much more abundant. A similar phenomenon is seen in the case of the *Microsphaera* on *Berberis* referred to below, and may be comparable in a way to that seen in the Erysipheae inhabiting the hexenbesen of *Phytoptus* on *Celtis*, or the erinoses of *Fagus* and *Cephalanthus*. When examined microscopically, this fungus proved to be an *Uncinula* almost as peculiar as the *Taphrina* with which it was associated, owing to the very unusual modification of its appendages, which become distally twisted in a close spiral of striking appearance. The perithecia (fig. 7), which are usually epiphyllous, although sometimes amphigenous, are often densely crowded, of a reddish-brown color, globose-depressed, coarsely areolate. They show considerable variation in size (70–100 μ), and in the number of asci (5–8) contained in each. The appendages (figs. 7, 8) are 4–8 in number, without septa, the basal portion thick-walled and suffused with reddish brown, the suffusion involving also one or sometimes more than one turn of the spiral portion, which is otherwise quite hyaline and may show as many as eight turns, sometimes but half this number, ending in a helicoid extremity (figs. 8, 9), of characteristic contour, thin-walled, and somewhat inflated. The appendages are quite rigid, and curve somewhat upward from their insertion on the equatorial region, whence it is evident that the twisting does not assist in freeing them from the substratum, but, if it has any significance, must be supposed to enable them to become more readily attached to objects with which they may come in contact. A somewhat similar phenomenon is seen in *Sphaerotheca spiralis* Neger, discovered by DUSEN on *Escal-*

lonia rubra near the Lago Argentina in Patagonia, and very kindly communicated to me by Dr. NEGER. The spiral twisting of the appendages in this form, although distinct, is, however, more or less indefinite and decidedly irregular. A somewhat similar tendency is also seen in other species of *Uncinula*, and a variety on poplar of the common *U. salicis* has been distinguished as *U. heliciformis* by E. C. HOWE, owing to a similar though slight tendency to the production of a terminal spiral in the appendages. It seems certain, however, that no species of *Uncinula* hitherto described could be interpreted with sufficient liberality to include this antarctic form which may be characterized as follows:

Uncinula Nothofagi, nov. sp.—Epiphyllus vel rarius amphigenus: peritheciis mycelio albido persistenti effuso insedentibus, dense congestis vel discretis, globoso-depressis, 80 μ diam. (70–100 μ), rufo-brunneis, cellulis 10–20 μ diam.: appendicibus 5–15, aseptatis, 70–100 μ longis, inferne rectis vel curvatis, rigidis, induratis, brunneo-suffusis; superne spiraliter arcte 4–8 convolutis, apice helicoideo-subinflatis, spiris basalibus plus minus suffusis, ceteris hyalinis: ascis late ovalibus, 5–8 in quoque perithecio, suboctosporis; sporidiis oblongo-ellipsoidiis 18–20×10 μ: conidiis subcylindraceis, 25–32×10–15 μ.

In foliis *Nothofagi antarcticae* var. *bicrenatae*, *Taphrina* occupatis vel rarius eis in folia sana migrans. Punta Arenas, Magellanes, Chile.

Much to my surprise, the *Uncinula* above described proved to be not the only species having this peculiar habitat, and among the small shrubby trees of *N. bicrenata* which grow to the south of the town in the califate pastures, I several times encountered a very different species, always on leaves attacked by the *Taphrina*. This form was decidedly rare and only a small amount of material was obtained by diligent searching. The two species were easily distinguished with a hand lens, the large perithecia of the second form being sparingly produced, its long irregularly flexed appendages, which in many perithecia are undeveloped, lacking the spiral coils of its ally and ending in an open hook, or half-helix, more or less characteristic in contour, and recalling the tip of a golf stick or the curved handle of an umbrella (fig. 12). In general these appendages are decidedly more than twice as long as the

diameter of the perithecium (fig. 11), quite hyaline, their outline somewhat uneven with an occasional slight irregular swelling. The perithecia which almost always occur on the upper side of the leaf, as far as I have seen, are much larger than those of *U. Nothofagi*, and contain many more (10–20) asci, each with three or four spores instead of eight. Since it does not seem possible to refer this form to any of the described species of *Uncinula* it may be characterized as follows:

Uncinula magellanica, nov. sp.—Plerumque ephiphyllus. Peritheciis mycelio albido effuso exiguo insidentibus, discretis vel subgregariis, globoso-depressis, opacis vel subopacis, atro-brunneis, 130 μ (90–150 μ) diam., cellulis 10–20 μ latis; appendicibus 10–22, hyalinis, longis, tenuibus, curvatis vel subflexuosis, subrigidis, 225–400×5–6 μ, apice subinflatis et subrecurvatis: ascis late clavatis, 55×25 μ, plerumque 3–4 sporis, sporidiis 20×10–12 μ: conidiis subcylindraceis, 35–40×15–18 μ.

In foliis *Nothofagi antarcticae* var. *bicrenatae*, *Taphrina* obsessis. Punta Arenas, Magellanes, Chile.

Three other species of Erysipheae were also found in the neighborhood of Punta Arenas. Of these a form, encountered but once on a species of *Galium*, appears to be *Erysiphe Chicoracearum;* while another not uncommon on several Compositae does not seem to differ from *Sphaerotheca fuliginea*. The third, however, is quite remarkable on account of its habitat; since, like the two species of *Uncinula* just described, it appears to be invariably associated with another fungus. Toward the end of February I noticed that the distortions on *Berberis buxifolia* caused by *Aecidium magellanicum* were assuming a whitish appearance from the invasion of an *Oidium* that covered the leaves and twigs which were attacked by the rust; and early in March it was almost impossible to find a specimen that was not more or less completely covered by it. I looked in vain for perithecia, however, and it was not until the very last days of my stay (March 10) that I was able to obtain a rather scanty supply of leaves bearing scattered perithecia, many of which were fully matured. The latter proved to belong to a species of *Microsphaera* which I am unable to distinguish from *M.*

Alni. Indeed it appears to be closer to the typical form of this species than most of the varieties of the latter. The habitat, however, is certainly remarkable; and although I made a special effort to find even the *Oidium* apart from the *Aecidium*, I never succeeded in doing so.

I find but one other species of this family recorded from Punta Arenas, in fact the only other species, I believe, which has been hitherto recorded from this locality. This was found by SPEGAZZINI on *Ribes magellanicum* and is mentioned in his *Fungi Patagonici* (p. 34). It was also found by him on the same host in Tierra del Fuego and described as *Phyllactinia antarctica* Speg., a name which is not recognized in SALMON'S *Monograph*, where it is placed as a synonym of *P. Corylea*. Although *Ribes magellanicum* was not uncommon along the ravine of the Rio de las Minas, I did not discover this *Phyllactinia*, not being aware at the time that it should be sought for on this host.

HARVARD UNIVERSITY

EXPLANATION OF PLATES XVIII AND XIX

The figures were drawn with camera lucida from preparations, in glycerin, of sections cut from dried material, and are reduced about one-fourth. The following combinations of objectives and oculars were used in making the drawings: figs. 1, 2, Zeiss D, oc. 4; figs. 3–6, Leitz water immers. 10, oc. 4; fig. 7, Leitz C, oc. 4; figs. 8–10 and 12, 13, Leitz water immers., oc. 1; fig. 11, Zeiss A, oc. 4.

PLATE XVIII

Taphrina entomospora Thaxter

FIG. 1.—Portion of the lower surface of a leaf showing the ascus primordia lying between the cutis and the epidermis; one at the right beginning to develop.

FIG. 2.—Portion of section showing asci.

FIG. 3.—A single ascus containing eight ascospores which have not yet begun to bud.

FIG. 4.—A more mature ascus in which the spores have developed their characteristic appendages.

FIG. 5.—Three ascospores in which the appendages are in process of formation.

FIG. 6.—Six mature or nearly mature spores with their appendages.

PLATE XIX

Uncinula Nothofagi Thaxter

FIG. 7.—Two perithecia showing variably developed appendages, the upper shown in surface view, the lower showing the appearance of the eight asci seen partly in optical section.

FIG. 8.—A single well developed appendage enlarged.

FIG. 9.—The tips of two appendages enlarged.

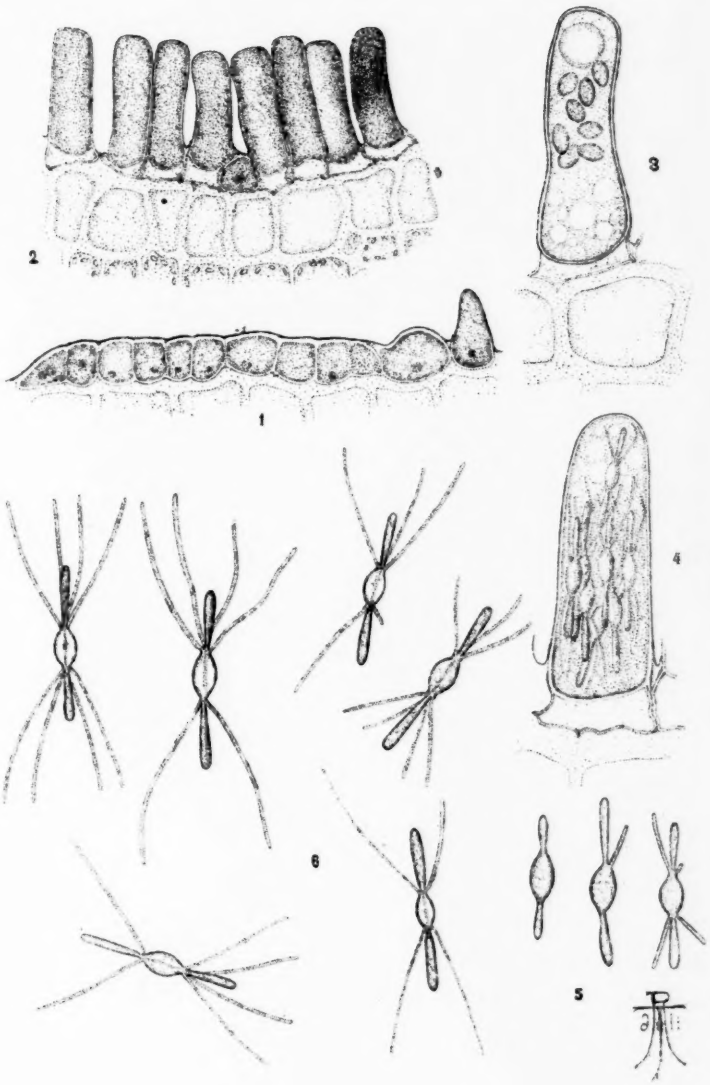
FIG. 10.—Two asci.

Uncinula magellanica Thaxter

FIG. 11.—A single perithecium.

FIG. 12.—A single appendage and three tips of appendages enlarged, showing variations in the terminal hooks.

FIG. 13.—Two asci.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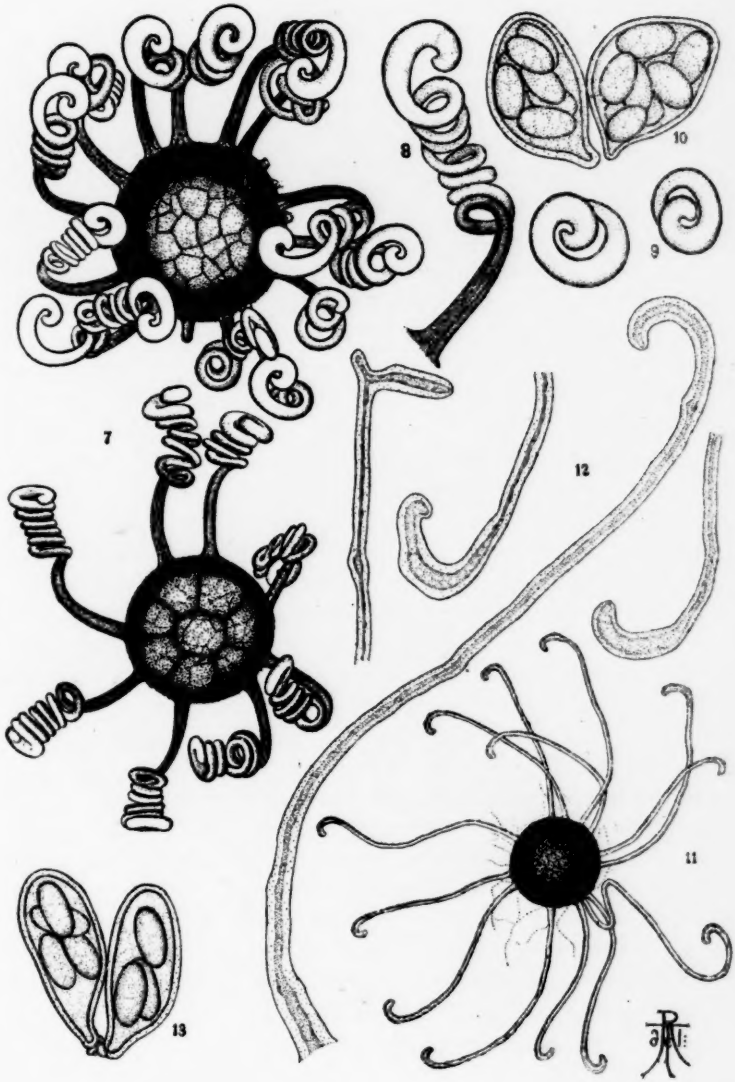
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THE DEVELOPMENT OF THE ASCOCARP OF LEOTIA[1]

WILLIAM H. BROWN

(WITH FORTY-SEVEN FIGURES)

The present study is based upon material of *Leotia lubrica* and *L. chlorocephala* collected at Cold Spring Harbor, Long Island. For microscopical study, sections were cut 2 and 3 μ thick and stained with either Haidenhain's iron-alum hematoxylin or Flemming's triple stain.

Leotia lubrica

Leotia lubrica grows in damp places among various species of mosses. Several ascocarps are often connected together by their bases, and sometimes a small one may grow out from the base of a mature specimen.

The age of an ascocarp cannot always be told from its size, for one 3 mm. long may be more mature than one about 1 cm. in length. The youngest specimens found were about 1.5 mm. long, and were nearly conical in shape (fig. 1). When the ascocarp has reached a length of about 2 mm., the tip of the cone begins to enlarge to form the head (figs. 2, 3); this is about the stage at which the hymenium begins to be differentiated. The ascocarp soon assumes the mature form (fig. 4), and the further changes are largely those of growth. The hymenium now covers the upper surface and margin of the head. The upper surface may continue to grow until its margin becomes curved in toward the stalk (fig. 5).

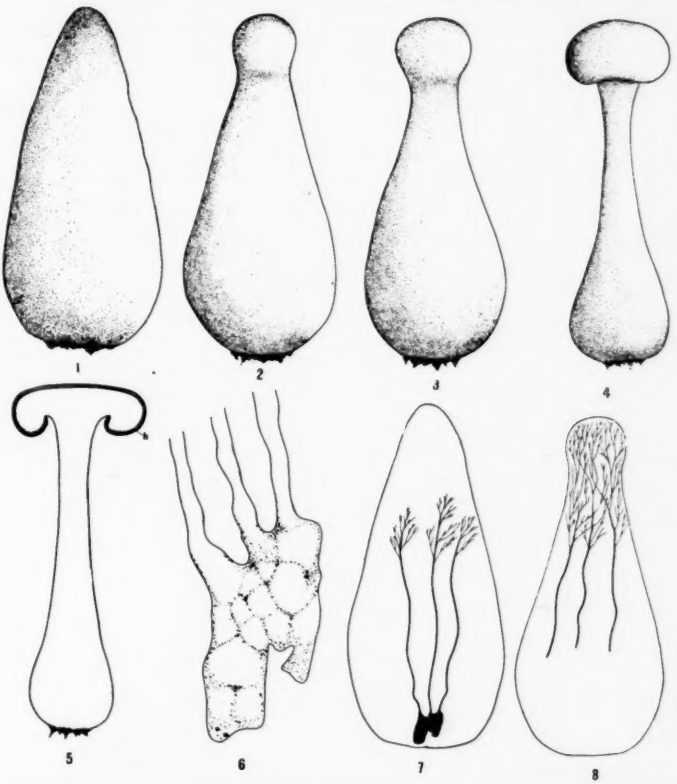
The youngest specimen found was composed largely of densely interlacing vegetative hyphae. At the base of the ascocarp there was a very large cell (fig. 6) from which a number of large hyphae extended upward toward the tip of the ascocarp. This large cell was vacuolated and its contents had degenerated, giving it all the appearances of an emptied ascogonium. The hyphae arising from this cell were empty, as is usually the case in old ascogenous hyphae, and so could not be traced with certainty for any great distance.

[1] Contribution from the Botanical Laboratory of the Johns Hopkins University, no. 17.

They appear, however, to be connected with similar hyphae which become very distinct only a little farther up (about 10 μ) in the ascocarp. These latter hyphae, of which there are three or four, are the ascogenous hyphae. They are very much larger than the surrounding vegetative hyphae, and in the character of their contents are quite distinct from them. The ascogenous hyphae become more and more distinct as they get nearer the tip of the ascocarp, but they show little tendency to branch until they have reached about one-half the distance from the base to the tip, when they divide to form a large number of smaller, much branching hyphae. These latter hyphae have a tendency to spread out as well as to grow upward, but in young specimens they are of course near the larger hyphae. Assuming that the large cell at the base of the ascocarp is an ascogonium, as seems to be the case, and that it is connected with the ascogenous hyphae, this stage may be represented diagrammatically as in fig. 7, in which the black lines represent the ascogenous hyphae. In slightly older specimens the ascogenous hyphae have spread over the entire tip. At about this time the tip enlarges to form the head of the ascocarp. Some of the vegetative hyphae soon grow out to form the paraphyses, after which the ascogenous hyphae give rise to asci. This stage is represented diagrammatically in fig. 8, in which the black lines still represent the ascogenous hyphae, the older parts of which have disappeared.

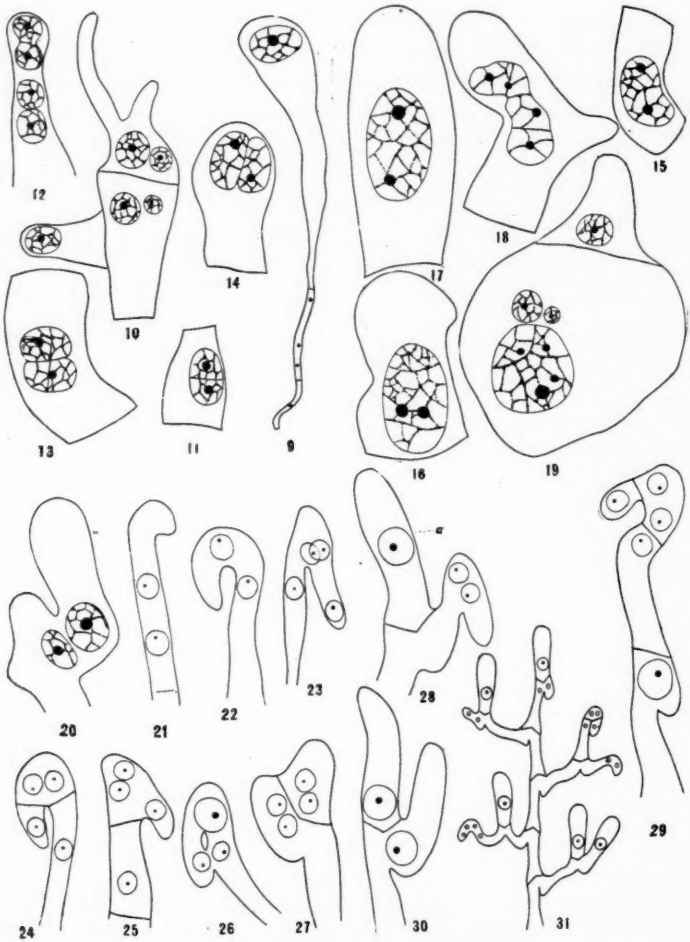
While the hymenium is being differentiated, some of the vegetative hyphae give rise to large storage cells (fig. 9). This process is similar in the two species studied and the same description will apply to both. These large storage cells are formed in rows and give rise to paraphyses (fig. 10). The storage cells are at first multinucleate, but the nuclei usually fuse as growth proceeds (figs. 11–14). This process continues until often the cells contain a single, very large nucleus, many times the size of the largest nucleus in the ascus (figs. 15–17). Frequently the nuclei are very irregular (fig. 18). In other cases, a cell may contain a very large nucleus with several much smaller ones lying near it (fig. 19). These last two cases suggest amitoses, but may very well be stages in fusion. The storage cells may have a very irregular shape

(fig. 20), or they may be quite regular (fig. 17). They are relatively much more abundant in young ascocarps than in the older ones. The storage cells seem to have the same function as the barrel-



FIGS. 1–8.—Fig. 1, young ascocarp, ×50; fig. 2, early stage in formation of head, ×37; fig. 3, older stage, ×30; fig. 4, mature ascocarp, ×3; fig. 5, longitudinal section of old ascocarp (*h*, hymenium), ×2.5; fig. 6, large cell at base of ascocarp, ×2100; fig. 7, diagram showing probable relation of ascogenous hyphae and ascogonium in young ascocarp; fig. 8, diagram showing position of ascogenous hyphae at time of formation of hymenium.

shaped cells described by HARPER (**16**) in *Pyronema confluens*, and are very much like similar storage cells in *Lachnea scutellata*. The chief difference seems to be that in *Pyronema confluens* and



FIGS. 9–31.—Fig. 9, vegetative hyphae giving rise to storage cell; fig. 10, paraphyses growing out from storage cells; figs. 11–14, fusion of nuclei in storage cell; figs. 15, 16, nucleus with two nucleoli in storage cell; fig. 17, large storage cell with single very large nucleus; fig. 18, storage cell with very irregularly shaped nucleus; fig. 19, storage cell containing one large and two small nuclei; fig. 20, an irregularly shaped storage cell; figs. 21, 22, tip of ascogenous hypha with two nuclei; fig. 23, two nuclei in tip of hypha have divided to four; fig. 24, walls have come in, separating sister nuclei; fig. 25, hook in which there is no wall cutting off uninucleate ultimate

Lachnea scutellata the nuclei of the storage cells probably do not usually fuse.

The details in the formation of the asci were studied chiefly in *Leotia chlorocephala*, and will be described in connection with that species. The appearance of the hymenium suggests, however, that the process is similar in the two cases.

Leotia chlorocephala

The ascogenous hyphae in *Leotia chlorocephala*, as in *L. lubrica*, have their origin in the stipe. The hymenium is also formed in the same way that has been described for *L. lubrica*.

In 1894 DANGEARD described the asci of *Peziza vesiculosa* as originating from a binucleate penultimate cell of an ascogenous hypha. Since that time the same phenomenon has been described by various workers in a number of forms. A large number of these are mentioned by OVERTON (**23**). The usual case seems to be that there are two nuclei in the tip of an ascogenous hypha. These divide simultaneously and walls come in between the sister nuclei of the two pairs, thus forming a binucleate penultimate cell and a uninucleate ultimate and antepenultimate cell. The ascus is then formed from the binucleate penultimate cell. MAIRE (**20**) and GUILLIERMOND (**14**) have described the asci of *Galactinia succosa* as originating from a binucleate ultimate cell. In *Humaria granulata* (BLACKMAN and FRASER **4**) the asci usually arise from a binucleate penultimate cell, but in two cases the asci had a terminal position.

In speaking of *L. chlorocephala* and a number of other ascomycetes, FAULL (**11**) says: "It is quite probable that the only

cell; fig. 26, hook in which two nuclei have fused to form nucleus of ascus, and tip has fused with stalk of hook; fig. 27, ultimate cell has fused with antepenultimate; nucleus of latter has migrated into former, which is growing out to give rise to ascus or another hook; fig. 28, two nuclei of penultimate cell have fused to form nucleus of ascus; ultimate cell has fused with antepenultimate, and nucleus of latter has migrated into former, which has grown out to form another hook; fig. 29, binucleate penultimate cell has given rise to hook; ultimate cell has fused with penultimate, and the two nuclei have fused; ultimate cell has not developed further; fig. 30, binucleate penultimate cell has formed ascus, which fusion product of ultimate and antepenultimate has given rise to second ascus; fig. 31, diagram illustrating multiplication of number of asci by method shown in figs. 26–30; figs. 9–20, ×1400; figs. 21–30, ×2100.

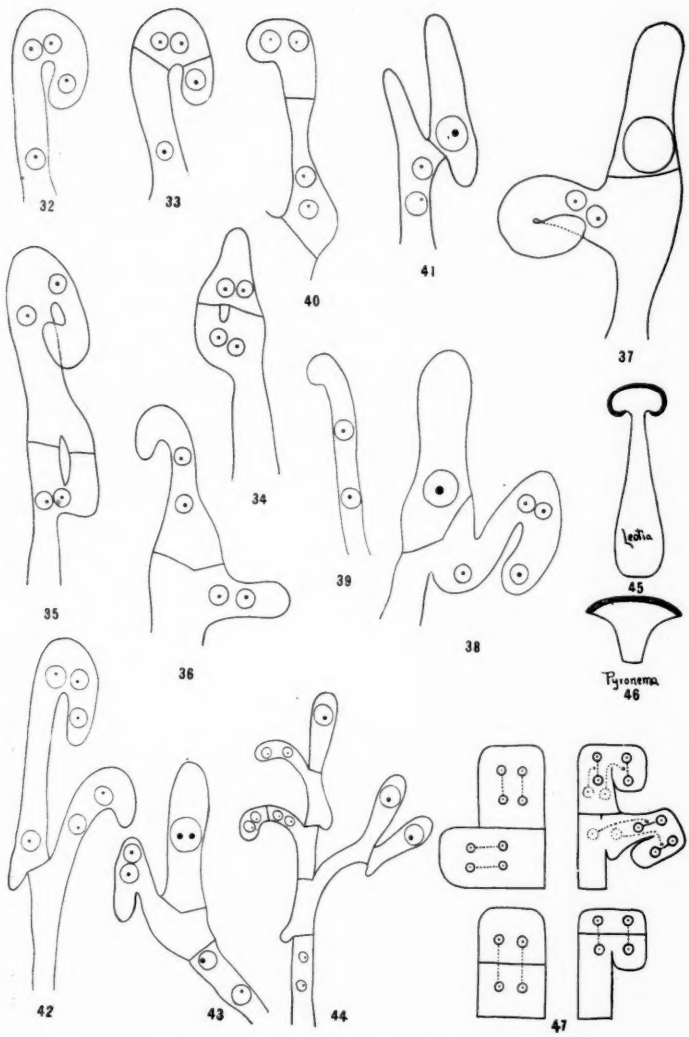
departure from the type is the lack of the cross wall that cuts off a uninucleate cell at the tip of the hypha." Later on he says that in some of the species the cross wall may be exceptionally present. In this statement he probably includes *L. chlorocephala*, as the cross wall is frequently present in this species. *L. chlorocephala*, however, shows quite a number of other deviations from what has been regarded as the usual type.

The tips of the ascogenous hyphae in the hymenium usually contain two nuclei, and become shaped like a hook (figs. 21, 22). The nuclei then divide, giving rise to four nuclei (fig. 23). Walls may then come in between the sister nuclei (fig. 24), or the wall cutting off the terminal cell may not be developed (fig. 25), or in still other cases both walls may be lacking even after the two nuclei in the bent portion of the hook have fused to form the nucleus of an ascus (fig. 26). When the nuclei are distributed as in figs. 23, 24, so that one is in the tip and two in the bent part of the hook, the two nuclei (apparently not sisters) in the bent portion may fuse to form the nucleus of an ascus (figs. 26, 28*a*), or they may give rise to the four nuclei of another hook (fig. 29). The uninucleate tip usually grows down and fuses with the stalk of the hook (fig. 26). The nucleus of the stalk may then migrate out into the tip (fig. 27), which usually grows out to form another hook (fig. 28), or sometimes an ascus (fig. 30). That in these cases it is the tip which has developed below the ascus is shown by the presence of the curved end of the tip joined to the stalk cell, as well as by the presence of both the wall which separated the ultimate cell from the penultimate and the one which divided the penultimate from the antepenultimate. The nucleus from the tip of a hook may occasionally migrate into the stalk. Sometimes the nucleus formed by the fusion of the nuclei of the tip and stalk does not develop further (fig. 29). This is usually associated with a vacuolated condition of the cytoplasm which indicates that the failure of the tip to develop is due to a lack of food. The processes described above, by which either the tip or bent portion of a hook may form another hook, are apparently often repeated many times, so that even in a young stage of the hymenium five or six hooks are frequently seen joined together in various ways. This is shown diagrammatically in fig. 31.

This same method of multiplication of asci occurs in *Geoglossum* sp. (figs. 32–38). The two nuclei in the tip divide to four (fig. 32) and walls come in between the nuclei of each pair of sisters (fig. 33). The antepenultimate cell may then form an ascus (figs. 37, 38) or another hook (figs. 35, 36). The ultimate cell usually fuses wlth the stalk (figs. 34, 35). The nucleus of the ultimate cell may then migrate into the antepenultimate (fig. 35), but usually the nucleus of the antepenultimate cell migrates into the ultimate (fig. 34), which then grows out (fig. 36) to form a hook (figs. 37, 38) or an ascus.

The phenomena connected with the formation of the asci as just described in *Leotia* and *Geoglossum* have been observed by the writer in *Lachnea scutellata*, as reported before the Botanical Society of America at the 1909 meeting (6). In a paper read at the same time before Section G of the A.A.A.S., McCubbin (21) described the penultimate cell of the ascogenous hyphae of *Helvella elastica* as forming either an ascus or a hook. The ultimate cell frequently fuses with the antepenultimate, after which the nucleus of the antepenultimate migrates into the ultimate. The two nuclei then migrate into a process which grows out from the ultimate to form another hook. In *Humaria rutilans* Miss Fraser (12) has described the uninucleate ultimate cells of the ascogenous hook as growing out to form other asci. She says that where such proliferation had taken place the tip was usually connected with the stalk, and in one case the nucleus of the tip was migrating into the stalk. She did not determine, however, whether or not the nucleus of the stalk took part in the formation of new asci. It seems probable, however, that she has observed something of the same phenomenon that has been described in *Leotia*. The writer (5) has described the ultimate cell of *Pyronema confluens* as growing out to form other asci. In such cases a nucleus could not be found in the stalk cell, and so it may be that it had migrated into the ultimate cell and had then taken part in the formation of the hook. The presence of these phenomena in such rather distantly related species as those mentioned above suggests that they may be of rather frequent occurrence.

Remembering that the nuclei in the binucleate antepenulti-



FIGS. 32–47.—Figs. 32–38, *Geoglossum* sp.; fig. 32, four nuclei in tip of hook; fig. 33, walls have come in between nuclei; fig. 34, ultimate cell has fused with stalk; fig. 35, binucleate penultimate cell has given rise to hook, while ultimate has fused with antepenultimate; fig. 36, binucleate penultimate cell has formed hook, and ulti-

mate cell are not sisters, but are composed of one nucleus from each of two pairs of sisters, it will be seen that every time either the ultimate or penultimate cell, if formed in the manner described above, gives rise to a hook, the distance of the relationship of the nuclei which fuse to form the nucleus of the ascus is increased. This can hardly be of any significance, however, in the case of *L. chlorocephala*, for, as will be shown later, two nuclei which are apparently sisters often fuse to form the nucleus of an ascus. It seems probable, therefore, that in *Leotia* the only use of the continued growth of the ultimate and penultimate cells is to increase greatly the number of asci which can be formed from a single hypha.

In *L. chlorocephala* the asci are also formed by another method, which probably occurs about as frequently as the one already described. In this case the tip of the hypha does not bend as much as in the first (fig. 39). When the nuclei have divided, a wall comes in between the two pairs of sister nuclei (fig. 40). That the two nuclei in each cell are sisters would seem to be shown by the fact that the hyphae appear to be too narrow to allow a side-by-side division of the nuclei, or for the nuclei to migrate past each other. There is, moreover, no evidence that such a parallel division or migration of the nuclei does occur. The two nuclei of the ultimate cell may fuse to form the nucleus of an ascus (fig. 41), or they may give rise to the four nuclei of another hook (fig. 42). That the asci and hooks in these cases are formed from a binucleate terminal cell is shown by the presence of the tip of the

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mate has grown out; figs. 37, 38, binucleate penultimate cell has formed ascus, while ultimate with nucleus from antepenultimate has given rise to hook; fig. 39, tip of ascogenous hypha with two nuclei; fig. 40, the two nuclei have divided to four and a wall has separated the two pairs of sister nuclei; fig. 41, two nuclei of ultimate cell have fused to form nucleus of ascus; penultimate cell is growing out to give rise to hook or ascus; fig. 42, both ultimate and penultimate cells have formed hooks; fig. 43, penultimate cell (*a*) has not developed further, while ultimate has given rise to hook similar to that shown in fig. 24; binucleate penultimate cell of this hook has formed ascus, while ultimate and antepenultimate have given rise to still another hook; fig. 44, diagram illustrating multiplication of asci by method shown in figs. 39–43; fig. 45, diagram of structure of ascocarp of *Leotia;* fig. 46, diagram of structure of ascocarp of *Pyronema omphaloides;* fig. 47, diagrammatic comparison of conjugate divisions in *Leotia* and in the rusts; figs. 32–43, ×2100.

hook at their bases. The binucleate penultimate cell may also grow out (fig. 41) to form a hook (fig. 42), or sometimes an ascus. In other cases it does not develop further (fig. 43). When this occurs the two nuclei may or may not fuse. Fig. 43 shows a case in which two binucleate cells were formed, the terminal one of which developed into a three-celled hook of the type first described. This hook then gave rise to an ascus and a second hook. It is clear from this that the same hypha may behave differently at different times. The formation of two binucleate cells may be repeated several times, as is shown diagrammatically in fig. 44.

In *Verpa bohemica*, FAULL (11) found the asci connected with the first, second, third, or fourth cell from the tip, but did not determine whether the asci grew out from the third or fourth cell, or whether the terminal cell underwent division after the budding out of the ascus.

In *Anixia spadicea* and *Urnula craterium*, FAULL (11) says that it looks as if the ascus might spring from any cell whatever. Judging from FAULL's figures, all of the above cases might perhaps be explained as due to the two methods of multiplication of asci described in *Leotia*.

In *L. chlorocephala* the ascus soon after its formation grows out into a much elongated cell. Its nucleus divides three times, in the manner usual among the nearly related Pezizineae, and gives rise to the nuclei of the eight spores. The spores are at first round, but by subsequent growth they become elongated and vacuolated.

Systematic position of Leotia

ENGLER (10) places *Leotia* in a group near the Pezizineae. The observations recorded above seem to confirm this view of the near relationship. The large cell, probably an ascogonium, at the base of the ascocarp and the presence of the ascogenous hyphae in the stipe suggest a homology with those Pezizineae in which the asci are formed from a single ascogonium, as *Lachnea scutellata*, *Peziza granulosa*, *Ascobolus pulcherrimus* (WORONIN 29), *Ascobolus furfuraceus* (JANCZEWSKI 17, HARPER 15, WELSFORD 28), *Ascodemus nigricans* (VAN TIEGHEM 27), *Ryparobius* sp. (BARKER 1),

Thelebolus stercoreus (RAMLOW 24), *Humaria granulata* (BLACKMAN and FRASER 4), *Lachnea stercorea* (FRASER 13), and *Ascophanus carneus* (CUTTING 7).

As has already been pointed out, the origin of the hymenium, including the storage cells and the formation of the asci, is also similar to the same process in some of the Pezizineae.

The presence of an elongated stipe, moreover, is of frequent occurrence among the Pezizineae, while a tendency of the hymenium to become recurved is shown by many of them. A comparison of figs. 45 and 46 will show the similarity in form between *Leotia* and an old specimen of *Pyronema confluens*.

From the above considerations it would seem that *Leotia* is as closely related to some of the Pezizineae as some of them are to each other, and it is probable that the ancestors of *Leotia* were closely similar to some of them.

Relationship of the fusing nuclei

According to what is probably the most prevalent interpretation, the fusion in the ascus is regarded as being of a vegetative character, and so the relationship of the fusing nuclei is considered to be of no great significance. This interpretation is based on the presence of a supposed fusion of nuclei in the ascogonium. Such fusions have been described in *Pyronema confluens* (HARPER 16), *Humaria granulata* (BLACKMAN and FRASER 4), *Lachnea stercorea* (FRASER 13), *Ascobolus furfuraceus* (WELSFORD 28), *Humaria rutilans* (FRASER 12), and *Ascophanus carneus* (CUTTING 7). CLAUSSEN (8), however, after a study of *Pyronema confluens*, has come to the conclusion that the fusion in the ascus is the only one that occurs in that species. BROWN (5) has described a form of *Pyronema confluens* in which the antheridium does not fuse with the ascogonium, and in this case he fails to find a fusion of nuclei in the ascogonium. The cytology of the ascus confirms this interpretation. There are, however, appearances in this form very much like fusing nuclei, which are due, however, to the fact that the daughter nuclei reorganize close together. BARKER, in studying *Monascus*, failed to find a fusion of nuclei in the ascogonium, but attributed this to his failure to get the proper stages. SCHIKORRA

(25) describes the fusion of the antheridium and ascogonium in *Monascus*, but does not find any fusion of nuclei except in the ascus. In *Lachnea scutellata* the writer has been unable to find any fusion of nuclei except the one in the ascus. The haploid number of chromosomes persists throughout the vegetative hyphae, ascogonium, and ascogenous hyphae; while the diploid number exists only in the primary nucleus of the ascus. There are, however, appearances in the ascogonium and other parts of the ascocarp, which were at first mistaken for fusing nuclei. When the nuclei are preparing for division, the chromosomes tend to become arranged in a group resembling a nucleolus. The nuclei at this stage are of course large, and often, unless well stained and carefully studied, appear to have two nucleoli. When the nucleoli have divided, they often reorganize so close together that after a slight growth they are pressed against each other as in the case of fusing nuclei. Careful study, however, has failed to show any cases in which the nuclear walls were disappearing, and often the remains of spindle fibers could still be distinguished. Even the nuclei resulting from the division of the primary nucleus of the ascus can sometimes be found pressed against each other. Considering the above facts and the increasing amount of negative evidence, it would seem necessary to study the nuclei in all stages, including division, and to distinguish between true and apparent fusions before the fusion of nuclei in the ascogonium can be regarded as proved or even probable. This is particularly true of such an aberrant case as the presence of a second nuclear fusion following the sexual fusion in the life history of the same plant, and it is to be noted that divisions in the ascogonium have not been reported in any of the forms, mentioned above, in which a fusion of nuclei has been described in the ascogonium. In view of what has been said, there would seem to be little reason for thinking that *Leotia* differs from *Monascus* and *Lachnea scutellata* in having a fusion of nuclei in the ascogonium; and so the explanation of the fusion of sister nuclei will probably have to be sought in some other way than by regarding the fusion as simply a vegetative one.

The question may be asked as to whether the relationship of fusing nuclei is of any significance if they are in the same plant

and are derived from a single nucleus with the haploid number of chromosomes. So far as the writer knows, there is no reason for thinking that there is. It is well known in agriculture that self-fertilization causes a diminution in the size and vigor of maize. SHULL (**26**) has shown that ordinary maize is a complex hybrid. If the elementary species are segregated out of the hybrid, self-fertilization has no bad effect, and it would seem that the deterioration of agricultural maize after self-fertilization is due to the segregating out of the smaller elementary species, which when recombined will again produce the more vigorous agricultural variety. According to the Mendelian interpretation, the harmful effect of self-fertilization in other genera is due to the same cause. The value of cross-fertilization for evolution is evident when we remember that it affords a means for trying a new character in a great number of combinations, one of which may finally be especially adapted to its environment. It may be that the persistence of cross-fertilization is due to its value in evolution, and that the presence of self-fertilization in such a relatively small number of the higher plants is due to the fact that such plants had less chance to interchange characters by crossing and so to develop along favorable lines.

It is evident that the above beneficial effects could not be produced by the fusion of distantly related nuclei if these were all in the same plant and were derived from a single nucleus with the haploid number of chromosomes, for even if the potentialities of one of the fusing nuclei were to be changed in some way, the change would probably be inherited by only one-half of the resulting progeny, and the nuclei of these would have the same potentialities as the changed nucleus and there would be no chance for further mixing. The end result would be the same if the nucleus whose potentialities had been changed had divided, and the two daughter nuclei had fused and given rise to the progeny. But even if a change in the fusing nuclei could be thought of as beneficial, there is no reason for thinking that such a change would occur. The work of JENNINGS (**18**) and JOHANNSEN (**19**) seems to show that the germ cells of organisms derived from a single pure individual are very rarely affected, even if the organisms

are subjected to different conditions and a rigorous selection practiced. In view of what has been said, we would not expect the relationship of fusing nuclei to make any difference if they were all in the same plant, and especially if they were all derived from a single nucleus with the haploid number of chromosomes. When therefore the ascogonium and antheridium, as in *Pyronema confluens* (HARPER 16), came to be derived from a single hypha, it would not seem to be a matter of great significance if the fusion of the nuclei derived from the ascogonium and antheridium should be replaced by the fusion of more nearly related or even sister nuclei, as seems sometimes to be the case in *Leotia chlorocephala*. It may be that the tendency toward the loss of sexual organs which is shown by a large number of the higher fungi is connected with the fact that there is in so many of them no provision for the fusion of nuclei derived from different individuals.

Conjugate division

In the first process of multiplication of asci described in *Leotia chlorocephala* there is a series of conjugate divisions comparable to those in the rusts. When the hook gives rise to a binucleate penultimate cell and a uninucleate ultimate and antepenultimate cell, and then the ultimate cell fuses with the antepenultimate, there result two binucleate cells in which the two nuclei are derived one from each of two pairs of sisters. This is of course the relation that exists in the rusts. The processes in the rusts and in *Leotia* are compared diagrammatically in fig. 47. If in *Leotia* the nuclei divided side by side rather than one in the tip and the other nearer the base of the hypha, and the walls still came in between the sister nuclei, there would result a series of binucleate cells resembling very closely those in the rusts. Such a division in an ascomycete has been described by MAIRE (20) in *Galactinia succosa*.

The cells which fuse in the rusts are often derived from separate hyphae, but BLACKMAN (3) says that in some cases the fusing cells may be sisters, while OLIVE (22) figures two cases in which one nucleus is apparently migrating into an adjoining cell. The fusion of the ultimate and antepenultimate cells in the hooks of

the Ascomycetes is probably vegetative, and its replacement by the fusion of cells of separate hyphae or sister cells would give rise to a process quite similar to that in the rusts. While the above facts suggest a similarity between the Ascomycetes and the rusts, they do not appear to be sufficient to warrant the conclusion that the fusions and conjugate divisions in the two groups are phylogenetically related.

Summary

The ascogenous hyphae of *Leotia* have their origin at the base of the ascocarp, probably from a one-celled ascogonium.

The asci are formed at the tips of the ascogenous hyphae in several different ways. In some cases a hypha forms a typical hook, consisting of a binucleate penultimate and a uninucleate ultimate and antepenultimate cell. In this case the two nuclei of the penultimate cell may fuse to form the nucleus of an ascus, or they may divide and give rise to the four nuclei of another hook. The uninucleate ultimate cell usually grows down and fuses with the antepenultimate cell, after which the nuclei of the two cells may give rise to the nuclei of another hook, or they may fuse to form an ascus. The walls separating the nuclei may fail to be formed without affecting the fate of the nuclei. In this process there is a conjugate division comparable to that in the rusts.

Frequently the ascogenous hyphae do not become markedly bent, and in this case, when the two nuclei in the tip divide, a wall may separate two pairs of sisters. Either of these pairs may divide and give rise to the nuclei of another hook or fuse to form the nucleus of an ascus. Any of the methods described above by which the number of asci is increased may be repeated many times.

The relationship of the nuclei which fuse in a plant like *Leotia* is probably of no significance, since they are all in the same plant and are probably derived from a single nucleus with the haploid number of chromosomes.

The vegetative hyphae form large storage cells in the hymenium. The nuclei in these cells frequently fuse to form a single large nucleus.

The development of the ascocarp indicates that all of its struc-

tures are homologous with those of the Pezizineae, and that *Leotia* is closely related to the Pezizineae.

The writer is greatly indebted to Professor D. S. JOHNSON for valuable suggestions and criticisms, and to Professor C. B. DAVENPORT for courtesies shown him during his stay at the Biological Laboratory of the Brooklyn Institute at Cold Spring Harbor.

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BRIEFER ARTICLES

THREE INTERESTING SPECIES OF CLAVICEPS

(WITH EIGHT FIGURES)

One of the fungi most commonly met in North Carolina occurs in sclerotial form upon *Paspalum laeve* and *P. dilatatum*.[1] Over large areas every plant may bear spikes showing one or more of these sclerotia. In summer they are covered with a yellowish coat of spores, and the fungus has heretofore been variously designated as *Sclerotium Paspali* Schw.,[2] *Sphacelia Paspali* Bornet, and *Spermoedia Paspali* Fr. The species was used extensively by the authors in a physiological investigation,[3] and is well represented in the accompanying photographs (figs. 1 and 2).

FIG. 1.—Sclerotia of *C. Paspali* as seen upon the host.

The abundance of the form and the fact that its perfect stage appeared to be unknown led us to attempt to grow from it an ascigerous stage. Numerous sclerotia which had wintered out of doors, naturally, were collected from the ground where they had fallen, and were planted on moist earth in glass capsules which were kept at room temperature. After about 20–25 days signs of germination appeared. Soon stalks 5–18 mm. long were developed, and on their ends round heads 1–2 mm. in diameter (fig. 3). By teasing or sectioning, perithecia and asci of the typical *Claviceps* form were found. But most remarkable, two clearly distinct types of perithecia, differing strikingly in size and shape, and bearing spores of decidedly different size, were found. The perithecia of the two forms are shown in figs. 4 and 5.

In the collection of the U.S. Department of Agriculture were found sclerotia from *Paspalum* bearing asci. These proved to be identical with the small-spored form of our own collection. Correspondence between

[1] These species were kindly determined for us by A. S. HITCHCOCK.

[2] FARLOW, Host index, p. 153; also SACC. Syll. Fung. 14:1152.

[3] Variation of fungi due to environment. BOT. GAZETTE 48:1–30. 1909.

Professor ROLFS and the Department of Agriculture, which has kindly been placed at our service, shows that Professor ROLFS at Clemson in 1901 noted the ascigerous stage of *Sclerotium Paspali* Schw. on *P. dilatatum*, and further observed that the ascospores were disseminated largely by beetles, principally of the family Carabidae, which running over the ground came in contact with the spores, and later in seeking a high point from which to fly would run up the culms, over the pistils, and thus bring about infection of the ovaries.

FIG. 2.—Sclerotia of *C. Paspali* upon the host, enlarged.

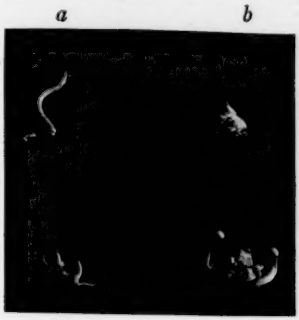

FIG. 3.—Sclerotia of *Claviceps* germinated: *a*, *C. Rolfsii*; *b*, *C. Paspali*.

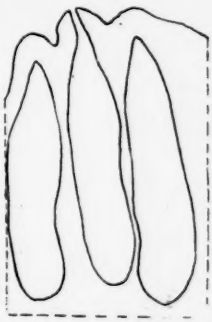

FIG. 4.—Perithecia of *C. Rolfsii*; magnification as in fig. 5.

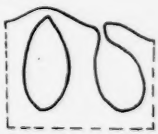

FIG. 5.—Perithecia of *C. Paspali*; magnification as in fig. 4.

Since the two species of *Claviceps* under discussion differ markedly from any heretofore described, and from the only *Claviceps* upon *Paspalum* (*C. lutea* A. Möll.), and from each other in many essential characters, prominently so in length of stipe and size of perithecia and spores, we herewith propose them as new species; the small-spored form as *C. Paspali*; the large-spored form as *C. Rolfsii*. The relation of these two species to *Sclerotium Paspali* Schw. is not definitely known. Both of them are associated with what has heretofore been known as *S. Paspali* Schw. It seems probable, therefore, that two sclerotial forms very closely resembling each other

FIG. 6.—*C. Tripsaci* upon the host.

have been included under the one name *Sclerotium Paspali;* but careful cultural studies and infection experiments alone can reveal the true relationship. That *Sclerotium Paspali* really belongs to the form-genus *Sphacelia*, where it was placed by BORNET, is also clear, possessing as it does small ovoid conidia borne upon simple slender stalks.

Claviceps Paspali, n. sp.—Sclerotia yellow to gray, globose roughened when mature, about 3 mm. in diameter; head dull yellow; stipe short to medium, usually not more than 1 cm. long, filiform; perithecia completely covering head, numerous, oval, 340×119 μ; asci cylindrical, 174 μ long; spores filiform, 101×0.5–1 μ.

Claviceps Rolfsii, n. sp.—Sclerotia yellow to gray, globose roughened when mature, about 3 mm. in diameter; head dull yellow; stipe filiform but thicker than in *C. Paspali*, 1–1.5 cm. long; perithecia few in head and mostly upon extreme distal portion, cylindrical ovate, 816×225 μ; asci cylindrical, 375×3 μ; spores filiform, 260–275×0.5–1 μ.

Upon gama grass (*Tripsacum dactyloides* L.) in late summer, and well into winter characteristic fungous growths are often seen protruding from the basal, ovulate portions of the spike, sometimes nearly every spikelet being affected (fig. 6). The structures are white, 12–20 mm. long and about 2–3 mm. thick. Toward their tips they may be browned and more shrunken than in regions near their bases.

Examination of the affected spikelets shows the grain to be absent and its place to be occupied by a light-colored sclerotium approximately the shape of the grain of the

host. In general the appearance is that of a *Claviceps* sclerotium, except that it is pale and soft, the protruding horn being the remnant of the summer stage. Throughout the early part of the season the protruding part bears myriads of straight to lunulate spores, showing strong resemblance to the ordinary lunulate *Fusarium* spore. The internal portion remains sterile throughout the winter. The appearance throughout was so *Claviceps*-like that sclerotia were collected in autumn and wintered in an open-air hibernating house, then planted for germination in the same manner employed with the *Paspalum* sclerotia. After some 20 days the emergence of ascophore stipes was noted, and 5 days later the heads were well developed (fig. 7). A particularly striking feature is the tendency of the stipes to fork and produce two or even four heads upon the same stalk. Teasing or sectioning showed typical *Claviceps* perithecia (fig. 8) and asci. The species seems to be new and we describe it as *Claviceps Tripsaci.*

FIG. 7.—*C. Tripsaci:* sclerotium showing heads and stalks; ×2.5.

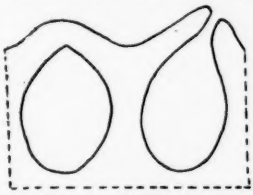

FIG. 8.—Perithecia of *C. Tripsaci;* magnification as in figs. 4 and 5.

Claviceps Tripsaci, n. sp.—Sclerotia smooth, white to dark brown or black, nearly conical, 4–5 mm. in diameter at base; heads gray to grayish white; stipe thick, white to purplish white, 1–1.5 cm. long; perithecia numerous, elliptical in longitudinal section, with a short beak toward the surface of the head, 390×153–187 μ; asci cylindrical, 145–175×2–3 μ; spores filiform, 130 μ long; conidia hyaline, continuous, fusoid to lunulate, 17.4–37.7×2.9–8.7 μ. —F. L. STEVENS and J. G. HALL, *N.C. Agricultural Experiment Station, West Raleigh, N.C.*

CURRENT LITERATURE

BOOK REVIEWS

Iron bacteria[1]

Coming from such authoritative source, this monograph ought to command the earnest attention of workers in the fields of science and of hydraulic and sanitary engineering; containing as it does so much that is of both scientific and practical interest, and embodying within its compass facts and deductions derived from the fruitful though laborious work of some eighteen years. The book is divided into seven chapters with the following titles: (1) The presence and distribution of the iron bacteria; (2) New iron bacteria, and a systematic review of known forms; (3) Pure culture methods; (4) The physiology of iron bacteria, and WINOWGRADSKY's hypothesis; (5) Other iron organisms; (6) Iron bacteria in relation to the production of bog iron ores; (7) The iron bacteria in their relation to practice: (*a*) rust formation in water pipes, (*b*) iron bacteria and the therapeutic use of chalybeate waters. In this review it will be possible to touch only upon the salient features of the treatise.

The author calls attention to the very wide distribution of the several species of iron bacteria, such as *Leptothrix ochracea*, *Cladothrix dichotoma*, *Crenothrix polyspora*, *Clonothrix fusca*, and *Gallionella ferruginea*, which occur in most bogs, ochre deposits, chalybeate springs, and stagnant waters, and at times in iron water pipes. As is well known, their presence in water pipes may create a veritable nuisance by the plugging of the pipes, or by rendering unfit for manufacturing purposes water that ought to be perfectly clear. It is pointed out as noteworthy that so far no iron bacteria have been recognized growing in sea water. To the six already well known species of iron bacteria, MOLISCH has added three others: *Chlamydothrix sideropus*, *Siderocapsa major*, and *Siderocapsa Treubii*, the last, curiously enough, being found growing on the submerged portions of certain aquatic plants, for example, *Elodea canadensis*, *Vallisneria spiralis*, and *Salvinia auriculata*. Doubtful recognition is extended by the author to certain new forms described by DAVID ELLIS. To obtain pure cultures of the various forms it is recommended that manganese peptone be used in combination with the native water and gelatin or agar, and the cultures should be grown at or about 25° C.

Considerable space is given to a discussion of the physiology of the iron bacteria, dealing particularly with the older and widely accepted theory of

[1] MOLISCH, HANS, Die Eisenbakterien. pp. vi+83. *col. pls. 3. figs. 12.* Jena: Gustav Fischer. 1910. *M* 5.

WINOGRADSKY that considers iron as a definite necessity for the carrying on of the vital processes of the bacteria. MOLISCH criticizes WINOGRADSKY'S work upon the grounds that that investigator did not work with pure cultures, and chose a bacterium (*Cladothrix dichotoma*) which did not actively store up iron as does one of the commoner forms (*Leptothrix ochracea*), so that his chances for accurate observation and deduction were sadly impaired. On the other hand, MOLISCH has worked with these organisms in pure culture, has demonstrated that they can grow readily enough on an iron-free medium, and that on examination of their protoplasm by microchemical methods no iron can be found. Further, he has shown that the iron bacteria can make use of manganese, as it occurs in water, in a similar way in which they use iron. According to the author, the iron in solution in the water is simply *deposited* in the viscid sheaths of the bacterial filaments in the form of soluble carbonate of iron, and through the action of the atmospheric oxygen it becomes altered to ferric oxid. This ferric oxid is in no discernible way utilized by the bacteria in their vital processes, but in its insoluble state acts as a protecting armor to the delicate protoplasmic filaments, pretty much in the same way as do the deposits or accumulations of silica in the case of the diatoms, or in the case of the epidermal cells of the grasses. When the bacteria use manganese, it is believed that that element is laid down in the sheaths in the form of manganese hydroxid, which under the action of the oxygen of the air is probably altered to manganic acid and finally to manganite.

The disappearance of the bacteria from waters that have been subjected to certain forms of treatment in which the iron is removed, MOLISCH explains in this way. Whether the form of treatment is that of filtration through sand or coke, or by chemical methods, great quantities of soluble organic materials in combination with hydrogen sulfid, ammonia, or carbonic acid are coincidentally removed, and this loss of organic materials is the real element determining the vanishing of the bacteria, inasmuch as it means the utter deprivation of the food supply, the absence of the iron being a matter of entire indifference. In the case of bog waters, the food supply is in the form of humus organic matters that are very readily removed by any method that removes iron. There exist in nature, MOLISCH states, other organisms than bacteria that are capable of fixing iron. These organisms are to be found among the algae, flagellates, and infusoria. His student ADLER has also demonstrated that some of them are able to fix manganese as well as iron. In all cases the *modus operandi* is quite similar to that of the bacteria.

Discussing the nature of the formation of deposits of ochre and bog iron, the author takes no dogmatic stand, but weighs the evidence in the light of the presence or absence of bacteria in material taken from such sources. The finding of bacteria in such deposits argues much for them playing at least a partial rôle in the formation, although it cannot be overlooked that there must be also a chemico-physical precipitation of insoluble iron due to the action of

the atmospheric oxygen and to the alkalescence of bog waters by aquatic plants. In rare instances the iron deposits may be made up almost entirely of the sheaths of the filamentous iron bacteria *Gallionella ferruginea* and *Leptothrix ochracea*. It may also be possible that deposits in which no bacteria may be found may have had their start by the growth of iron bacteria, but later on these may have died out and left no trace of their presence.

In regard to the formation of iron rust in water pipes, the author is in accord with the observations of the English investigator BROWN, and others, who believe that very often the incrustations of rust on the inner surface of the pipes may begin in areas accidentally left bare in the usual tarring process, and ferric oxid is formed by the action of the water entirely apart from the presence of iron bacteria, as the author himself has time and again demonstrated. It must be remembered, however, that where the presence of iron bacteria can be unequivocally established, there must occur the favorable combination of both soluble iron and organic food material; lacking the latter in sufficient quantity, no iron bacteria can gain a foothold.

MOLISCH very timely points out that much of the chalybeate waters bottled for medicinal purposes is worthless on account of the precipitation of the iron in insoluble form (ferric hydrate). This may be caused in one of two ways: (1) by the action of the air acting on the soluble iron carbonate, and (2) by the activities of one or other of the iron bacteria. This latter fact is established beyond a doubt, inasmuch as ADLER has cultivated iron bacteria from the waters of several chalybeate springs, and by the addition of various antiseptics has delayed the action of precipitation of the iron by inhibiting the growth of the bacteria. In practice such waters are recommended to be treated by filtration or by sterilization by heat.

The monograph is supplied with a full bibliography of the subject, and is plentifully illustrated with colored plates, original drawings, and photographs. The work constitutes a most valuable contribution to our knowledge of these peculiar and interesting microorganisms.—NORMAN MACL. HARRIS.

The morphology of gymnosperms[2]

In the present handsome volume the authors have more than doubled the size of their book on the same subject published almost a decade ago. It is a significant fact that the "fossil gymnosperms," relegated to an all too brief chapter in the earlier edition, are now distributed in accordance with their evolutionary sequence, and adequately and even copiously treated. The volume begins with the Cycadofilicales, as they are appropriately dubbed, in preference to the earlier and less suitable appelations Cycadofilices and Pteridospermeae. This group of gymnosperms, which has clearly emerged

[2] COULTER, J. M., and CHAMBERLAIN, C. J., Morphology of gymnosperms. pp. xi+458. *figs. 462*. Chicago: The University of Chicago Press. 1910. $4.10, postpaid.

from the paleobotanical limbo only within the decade, is given full consideration from every standpoint, and the account is made clearer for the general reader by an admirable summary of the general principles of fern anatomy. Next follow the Bennettitales, a group which American science has done so much to rescue from oblivion. In this as in the preceding chapter the authors have illustrated their account with good figures from original sources, and here we find the work of WIELAND, WILLIAMSON, and NATHORST freely drawn upon, just as SCOTT, OLIVER, KIDSTON, and POTONIÉ furnish the figures for the first chapter on the Cycadofilicales.

The treatment of the Cycadales is particularly full, as might be expected, in view of the special interest of the Chicago laboratories in the group. The illustrations comprise not only the gametophytes, but also the anatomy, which is more comprehensively dealt with in this instance than in the case of any of the other gymnosperms. This chapter must rank as perhaps the best in the volume. The Ginkgoales occupy about 35 pages. An interesting illustration here is a tone print of the identical tree from the botanic garden of the University of Tokyo, in the seeds of which HIRASÉ made the surprising discovery of spermatozoids.

The Coniferales naturally receive more attention than any of the older gymnosperms, since they are the prevailing naked-seeded plants of our epoch, and moreover are the exclusive representatives of the phylum in temperate climates. In the 140 odd pages devoted to the Coniferales, the authors discuss the order under the appelations customary in systematic accounts. It seems desirable as soon as possible to get rid of the inapposite and cumbersome appelations Pinaceae and Taxaceae, inherited from the taxonomic side, and replace them by other terms more in accordance with evolutionary lines in the Coniferales. Perhaps the time is not yet entirely ripe for that to be done. Although the conventional bifurcation of the Coniferales is adopted, the authors do not fail to discuss the hypothesis recently put forward by SEWARD, PENHALLOW, and the reviewer as to more appropriate groupings. It is recognized that the araucarian conifers stand in a group by themselves as compared with the Abietineae, Taxodineae, and Cupressineae. The authors even go so far as to grant, what seems inadmissible from the paleobotanical side, that the Araucarineae and pinoid conifers may have had an altogether separate origin from the Cordaitales. Nothing can apparently be clearer than that the earliest remains which can be referred either to araucarineous or abietineous affinities, have all the characteristics of conifers. The treatment of the coniferous series is particularly worthy of praise for its thoroughness and many-sidedness. The bane of morphology in the past has been the setting up of evolutionary hypotheses based on the consideration of facts of a single kind. This error has certainly been avoided here. The external habit, the spore-producing members, the vascular anatomy, the sporangia, the gametophytes, and the history or paleontological record of the group have all been considered. The result is one which,

although not without prudent reservations, is clear and along stimulating and evolutionary lines, with a due emphasis of principles and the avoidance of meaningless facts. What is most to be commended, and unfortunately a rare feature in botanical textbooks, is the recognition that stable results in connection with plant evolution can be built only on the firm basis supplied by the record of the rocks. Perhaps the only criticism which might be made of the long chapter on the Conifers is that it does not include among its many and good illustrations some of the anatomy of the group, especially as the importance of this phase of the subject is clearly and adequately recognized in the text.

About 40 pages are given to that fascinating and still, in spite of many recent additions to our knowledge, enigmatical group, the Gnetales. Presenting as it does so many characters, which ally it both with the gymnospermous and angiospermous seed plants, it is at once the lure and the despair of the morphologist. The conclusion is reached that the Gnetales rather represent a line of development from the same ancestry as the angiosperms, than a primitive group from which the higher seed plants have directly taken their origin. The authors seem to look with some degree of tolerance at least on the view, which has originated in recent years from added knowledge of the floral structure of the Bennettitales, to the effect that the angiosperms and Gnetales are an offshoot of the cycadophyte stock. This view of relationship rests entirely on the enigmatical inflorescence of the Bennettitales, and appears to have no support from a consideration of the structure of the gametophytes or the internal anatomy. While entertaining the possibility of a Bennettitean origin of the Gnetales, the authors at the same time suggest a possible derivation from the Coniferales. This is perhaps a more fruitful hypothesis, which may be justified when we possess some real knowledge of the past history of the group.

The volume reviewed is a masterly treatment of our present knowledge of the gymnosperms, and resumes in a particularly clear and happy way, from every standpoint, the evidence as to their structure, affinities, history, and evolution. It is vastly creditable to American morphology, and the statement may safely be made that there is nowhere in existence, at the present time, a general account of the group which is so judicial and authoritative, without being dull, hazy, or uninteresting. It follows of course that it is indispensable to every student of this important group of plants.—E. C. JEFFREY.

Vegetation der Erde

The ninth volume of ENGLER and DRUDE'S monumental work on the vegetation of the earth forms one of a series of monographic treatises that is to deal with the geographic features of the African flora.[3] Although the volume

[3] ENGLER, A., and DRUDE, O., Die Vegetation der Erde. IX. ENGLER, A., Die Pflanzenwelt Afrikas insbesondere seiner tropischen Gebiete. Band II. pp. xi+460. *pls. 16. figs. 316.* Leipzig: Wilhelm Engelmann. 1908. *M* 27 (subscription price *M* 18).

here under consideration is the first of the African series to make its appearance, it is logically the second, and will so stand in the completed work. The first volume is to give a general picture of the plant world of Africa, together with a survey of the ecological conditions. The following three volumes are to present detailed descriptions of the characteristic plants, especially of tropical Africa. The final volume is to deal with the plant formations and floral provinces.

For many years ENGLER and a number of collaborators have energetically exploited the flora of tropical Africa, especially that of the German possessions. The taxonomic results of this great undertaking have been presented from time to time, and now there is contemplated in these volumes a general summary of the large features of the African vegetation. The volume noted here gives an account of the pteridophytes, gymnosperms, and monocotyledonous angiosperms. For each family there is given a general account of its distribution and importance in Africa, following which is a more detailed description of the more important genera and species. The great wealth of illustrations, many of which are reproductions from photographs, makes this work the best source of ready information concerning the plants of Africa. Among the pteridophytes the Polypodiaceae play much the largest part. The gymnosperms are restricted to three genera each of cycads, conifers, and Gnetales. The grasses, which are presented by PILGER, have an immense number of forms, many of which are of great phytogeographic importance; the chief treatment of this great family is by plant formations rather than by taxonomic relationships. The numerous Cyperaceae are mostly hydrophytes. The palms, of course, are numerous, and are very characteristic of certain formations. The aroids are well developed, though less than in other tropics, and the epiphytic orchids are far less numerous and beautiful than in tropical America and Malaysia. The Liliaceae occur in great numbers and variety, the aloes in particular having a large display in xerophytic regions. Phytogeographers will await with eagerness the remaining volumes of this work.

In 1898 PAX issued the second monograph of ENGLER and DRUDE's *Vegetation der Erde*, presenting the general features of the vegetation of the Carpathian Mountains. There has appeared a second volume, which takes up certain detailed features of the same interesting region.[4] The first part considers the fossil flora of the Carpathians, especially that of the Tertiary and Post-Tertiary. The Tertiary flora is Upper Miocene, and much resembles the present Mediterranean flora, and as elsewhere in Europe is rich in forms that are now confined to America. It is interesting to note that in the warmer eastern Carpathians there are still some species which have remained as relicts from the Miocene. Since the ice age there has been in the western Carpathians

[4] ENGLER, A., and DRUDE, O., Die Vegetation der Erde. X. PAX, F., Grundzüge der Pflanzenverbreitung in den Karpathen. Band II. pp. viii+321. *map 1. figs. 29.* Leipzig: Wilhelm Engelmann. 1908. *M* 27.

a succession of forest forms, the birch and pine entering soon as pioneers; there followed then in turn the oak, the spruce, and finally the beech. The second part opens with a treatment of Carpathian genera which show slight variation, or which on the other hand are strikingly variable; this study results in interesting deductions of evolutionary importance, There follow a consideration of phenological phenomena, an account of the cultivated plants of the Carpathians, and a phytogeographical description of the thallophytes and bryophytes, which too often are ignored in such treatises. The treatment of the thallophytes is brief, owing to inadequate knowledge of their distribution, but the account of the bryophytes is more satisfactory. The western Carpathians are richer in bryophytes than the eastern Carpathians, owing to the greater rainfall and humidity. The third and final part treats in detail the particular features of the different districts of the Carpathians.—HENRY C. COWLES.

Plant anatomy

A second edition of STEVENS' *Plant anatomy*[5] has appeared three years after the first edition, which was reviewed in this journal.[6] That review stated fully the purpose and method of the book, so that only the notable new matter in the second edition needs notice here. It consists of a chapter of 38 pages on reproduction, and has been made imperative by the recent rapid development of plant-breeding as a science, involving as it does the fundamental principles of heredity. Professor STEVENS outlines first the mechanism of sporogenesis and of fertilization as now understood, and then presents in a clear and practical way the conclusions that have been reached by the application of MENDEL'S law. As said in the previous review, Professor STEVENS is an excellent teacher, and therefore, by text and apt illustrations, he has made an obscure region as luminous as it can be made for an elementary student.

As an elementary text on physiological anatomy, in which tissues and their functions are interwoven in their presentation, this volume is unique. It is not the new vascular anatomy, with its phylogenetic motive; or the old anatomy, with its deadness of detail; but the old "skeleton" animated by physiology and ecology rather than by evolution.—J. M. C.

MINOR NOTICES

Das Pflanzenreich.—Part 41[7] consists of a monograph of the Garryaceae, Nyssaceae, Alangiaceae, and Cornaceae by Dr. WALTER WANGERIN. In

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[5] STEVENS, WILLIAM CHASE, Plant anatomy, from the standpoint of the development and functions of the tissues, and handbook of micro-technic. Second edition. pp. xv+379. *figs. 152.* Philadelphia: P. Blakiston's Son & Co. 1910. $2.

[6] BOT. GAZETTE **46**:306. 1908.

[7] ENGLER, A., Das Pflanzenreich. Heft 41 (IV. 56[a]; 220[a, b]; 229). Garryaceae, Nyssaceae, Alangiaceae, Cornaceae, von WALTER WANGERIN. pp. 17, 19, 24, 110. *figs. 5 (26), 6 (47), 4 (38), 24 (193).* Heft 42 (IV. 147). Euphorbiaceae-Jatropheae, von F. PAX. pp. 148. *figs. 45 (155).* Leipzig: Wilhelm Engelmann. 1910. *M* 9.20; *M* 7.40.

these four families the author recognizes 15 genera and about 140 species. New species are published in *Garrya* and in *Alangium;* and several recently described species of *Cornus* have been incorporated and redescribed. The work is comprehensive, conservative in generic and specific limitations, copiously illustrated, and provided with excellent keys; it should serve as a valuable and authentic guide in the taxonomic study of plants belonging to these natural groups.

Part 42 embraces an exhaustive taxonomic treatment of the Euphorbiaceae-Jatropheae by Professor F. PAX. The tribe comprises 12 genera, and to these are referred 196 species, of which 43, or approximately one-fourth, are new to science. One new genus is included, namely *Neojatropha* of eastern tropical Africa, where it is at present represented by two known species. A second new genus (*Ritchieophyton*) is suggested and included in the key to the genera of the tribe, but publication of it is withheld for a subsequent fascicle dealing with this family. The group is treated in a masterly way, and numerous carefully executed original illustrations amplify the lucid text. Of considerable interest is the brief section dealing with geographical distribution. Seven of the twelve genera are exclusively American, while five (including *Ritchieophyton*) are paleotropic; and *Jatropha*, the largest of all the genera, extends throughout the equatorial belt. The two great centers of distribution of these plants in America are (1) in the region from Central America southward to Brazil and Paraguay, and (2) independently, in the West Indies.—J. M. GREENMAN.

A new flora of Congo.[8]—The present volume records all flowering plants of the Congo known up to the end of 1908, and includes a limited bibliography, citation of exsiccatae, and the vernacular names in many instances. The flora embraces a total of 3546 recognized species, of which 2826 belong to the dicotyledons, 717 to the monocotyledons, and 3 to the gymnosperms. The last group is represented by *Gnetum africanum* and two species of *Encephalartos*. The main elements of the flora, as represented by leading families, are as follows: Leguminosae (415 species), Rubiaceae (299), Orchidaceae (152), Compositae (148), Euphorbiaceae (144), Cyperaceae (139), and Gramineae (132). A very interesting tabulation is given showing the growth of our knowledge of the flora from 1896 to 1908. The work is well indexed, but is entirely without keys to genera or species. Brief keys leading to the species, particularly in the case of the larger genera, would have added considerably to the usefulness of the book.—J. M. GREENMAN.

Paleobotanical literature.—JONGMANS[9] has begun the publication of a very useful and a most laborious series, presenting a complete and well-organized

[8] DURAND, THÉOPH. ET HÉL., Sylloge Florae Congolanae. Bull. Jard. Bot. Brux. 2:1–716. Bruxelles: Maison d'édition A. Castaigne. Albert de Boeck, Successeur. 1910.

[9] JONGMANS, W. J., Die palaeobotanische Literatur. Vol. I. pp. iv+217. Jena: Gustav Fischer. 1910. *M* 7.

bibliography of paleobotany. The first volume contains the titles of 1908, and is divided into two sections: (1) an author list (pp. 17), which includes 309 entries; and (2) a subject list (pp. 200), by which one may find at once any plant referred to. The number of titles is increased by the fact that the list includes many papers on living forms which are related in some way to the interpretation of paleobotanical material. In these days, when paleobotany is becoming such a necessary part of morphology, such a volume has become indispensable.—J. M. C.

A revision of the genus Eucalyptus.—The title-page and index received recently completes the first volume of *A critical revision of the genus Eucalyptus* by J. H. MAIDEN.[10] In this volume the author treats 40 species, giving detailed descriptions, synonomy, distribution, and much supplementary information; these species and their known varieties and forms are illustrated by 48 admirable plates. The work is an exhaustive and authoritative treatment of this highly interesting and economically important group of plants, and it is a pleasure to note that it is being continued; the first part of the second volume, containing nine species and four plates, has already been issued.—J. M. GREENMAN.

Illinois State Academy of Science.—The third volume (1910) of Transactions contains the following botanical papers: The vegetational history of a blow-out (abstract), by H. A. GLEASON; Preliminary account of the forest successions on Isle Royale, Lake Superior (abstract), by W. S. COOPER; The forest associations of northwestern Illinois, by H. S. PEPOON.—J. M. C.

NOTES FOR STUDENTS

Plant diseases.—BANCROFT[11] has studied the life history of *Cladosporium herbarum* and finds that this fungus, known to be common on dead leaves, is connected with a parasitic stage which from its fructification would be classed in the form genus *Hormodendron*. The *Hormodendron* form makes holes in the leaves of many plants, among which are cucumber, melon, and cabbage. It is mentioned as epidemic in cucumber leaves. The holes are said not to be formed by the drying and falling out of areas of tissues, as in leaf-spot diseases. In this case the perforations occur from the first and increase in size, often running together so as to form large irregular holes. The margins are surrounded by a narrow line of dead brownish tissue. From the tissues surrounding the holes conidiophores of *Hormodendron* appear and produce branched chains of conidia. In cultures from these chains, conidia of *Hormodendron* were at first produced, but as the cultures became older only those of *Cladosporium* were formed.

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[10] MAIDEN, J. H., A critical revision of the genus *Eucalyptus*. 4to. pp. 349. *pls. 48*. Sydney: William Applegate Gullick. 1903–1909.

[11] BANCROFT, C. K., Researches on the life history of parasitic fungi. I. *Cladosporium herbarum* Link. Annals of Botany **24**:359–372. *pl. 1*. 1910.

It was found also that on dead or dying leaves infected with *Hormodendron* the conidia of that form gave way to fructifications of *Cladosporium*. It seems, therefore, that during the actively parasitic life of the fungus *Hormodendron* conidia are formed, but at the end of the growing season *Cladosporium* develops on the dead and fallen leaves. The conidiophores of *Cladosporium* arise from a sclerotium-like mass of fungous cells. The author finds that the cells of this sclerotium retain their vitality through the winter and give rise to conidiophores of *Cladosporium* in the spring. The disease is probably propagated by means of these sclerotia and conidia.

In order to describe the means by which some of the parasitic fungi whose ascospores are either not often found or are entirely unknown to persist through the winter, EWERT[12] has studied the effect of low temperature on the conidia of several species. The pycnidia of *Mycosphaerella sentina* Kleb. on fallen pear leaves left exposed during the winter were found to contain numerous conidia capable of germination during all the months of winter and as late as June, when new infections of the fungus appeared in the orchards. The temperature during the winter ranged as low as $-22°2$. Infection experiments with these conidia were not successful, but this the author attributes to faulty methods of manipulation. Infections with other conidia which had been exposed to low temperatures for a short time were successful. The conidia of *Pseudopeziza Ribis* Kleb. were also shown to retain their vitality through the winter. Conidia of *Fusicladium pirinum* and *F. dendriticum* subjected to low temperatures once or several times were still capable of germination, although in this case the matter is of less importance, since both of these fungi form ascospores regularly, and moreover have a perennial mycelium.

BROOKS and BARTLETT[13] report on two diseases of gooseberry bushes caused by *Botrytis cinerea* and *Cytosporina Ribis*. The first indication that plants are attacked by *Botrytis* is the wilting of one or more branches. Later the basal parts of such branches show great numbers of conidiophores of *B. cinerea* arising from sclerotia situated just outside of the woody cylinder. At this time it is found that the pith, wood, and bast are filled with mycelium. The fact that the wood is infected is particularly interesting, as *Botrytis* generally attacks only the soft parenchymatous tissues. It appears, however, that in this case lignified walls are not affected by the fungus, which makes its way through the vessels, and passes from cell to cell through the pits. The composition of the lignified tissues appears not to be changed. The food substances of the medullary rays are used up, but nothing is said of the contents of the wood parenchyma. Infections were produced by inserting into wounds

[12] EWERT, R., Die Ueberwinterung von Sommerkonidien pathogener Ascomyceten und die Widerstandsfähigkeit derselben gegen Kälte. Zeitschr. Pflanzenkrank. **20**: 129–141. *figs. 2.* 1910.

[13] BROOKS, F. T., and BARTLETT, A. W., Two diseases of gooseberry bushes. Ann. Myc. **8**:167–183. *pl. 1.* 1910.

small pieces of grape juice gelatin, in which the mycelium of the fungus was growing. Inoculation experiments with spores were not successful. The authors suggest that plants in nature may become infected through aphis punctures, the honey dew furnishing a means for the germination of the spores, or by means of frost injuries, or by accidental wounds made in picking the fruit. Since infection by any of these means was not demonstrated, and the authors' own infection experiments with conidia were unsuccessful, these suggestions would be more convincing if supported by more experimentation and less theory.

The disease produced by *Cytosporina Ribis* resembles in its general effects that caused by *Botrytis*. The infection takes place through a wound, as is shown by the universal occurrence of an old scar or dead stump at the point from which the disease spreads. Cross-sections of infected branches show that the wood is brown and discolored except for a lighter sector-shaped area. The wood is permeated with hyphae which, unlike those of *Botrytis*, are able to dissolve the lignified elements of the stem. The progress of the mycelium is accompanied by the formation of wound-gum which accumulates in the cells and vessels. The gum, at least in the wood parenchyma and medullary rays, appears to be formed from the starch. It seems that the accumulation of gum occurs only within the cells and does not involve the destruction of whole areas of tissues, as in most cases of gummosis.

McALPINE[14] reports a number of laboratory experiments with *Phytophthora infestans*, among which is an attempt to determine the possibility of destroying the mycelium in infected potato tubers without destroying the life of the tubers. Slices taken from diseased tubers were subjected to a temperature of 49° for four hours, and the fungus was found to have been destroyed. Afterward seed potatoes were subjected to the same heat and were found to sprout freely, hence the conclusion that seed potatoes can be thoroughly disinfected in the way described. It seems that the method should at least have been given a more extended trial to justify the conclusion, for it is not unlikely that whole tubers would be injured if subjected to that temperature long enough to kill the mycelium in their interior, although the mycelium might be readily killed in thin slices. The author does not state whether the slices in which the mycelium was actually killed retained their vitality through the treatment or not. Neither does he state that the seed potatoes used were diseased before the treatment and free from disease afterward.—H. HASSELBRING.

The species of Penicillium and Aspergillus.—The forms of Fungi imperfecti grouped under the name *Penicillium*, on account of their omnivorous habits, have served as subjects for numerous physiological investigations, but as a rule little attention has been given to the determination of the species in

[14] McALPINE, D., Some points of practical importance in connection with the life history stages of *Phytophthora infestans* (Mont.) DeBary. Ann. Myc. **8**:156–166. *pl. 1.* 1910.

this group. The genus has been as repellent to the systematist as it has been attractive to the physiologist. With the exception of the work of DIERCKX, only a brief abstract of which seems ever to have been published, there has been no effort to disentangle the mixture of forms of this genus. The efforts of THOM[15] toward clearing up this tangle and making possible the identification of forms will be welcomed, therefore, by botanists and especially by plant physiologists, who are now enabled to connect certain physiological activities with definite species.

The plan of the work has been to carry out on different media of known composition series of cultures of all forms obtainable, and base the distinction of species upon differences in the forms and in their reaction upon the media under similar environment. The method is essentially that which has enabled bacteriologists to classify the enormous number of forms with which they deal. By this method it is shown that the same species differs greatly in morphological characteristics and physiological reactions when grown on different media. Species that resemble each other upon one medium show marked differences upon other media. The characters of the plants are constant for each medium upon which they are grown. The cultural work of this investigation has extended over more than four years, and has resulted in the accumulation of many valuable physiological data which are conveniently tabulated at the end of the paper.

In the systematic part of the work 36 species and 3 varieties are carefully described and their reactions upon various culture media given. Of these, 13 species and 3 varieties are described as new; 9 are described under numbers, since the author feels that their characteristics are not yet sufficiently well known to warrant giving them names. Camera lucida drawings showing the modes of branching of the conidiophores, and other diagnostic characters are given for 33 species and the 3 varieties. The number of species described probably represents a large proportion of the known species of *Penicillium*. Many of them are described as new, but it may be that of these some are included in the 80 odd species in the *Sylloge*, for it is practically impossible, as the author has found in spite of the most painstaking attempts, to identify plants with older descriptions or herbarium material.

A work similar in nature, but far less in extent, was done by MANGIN[16] for a small group of molds of the genus *Aspergillus*. He takes up the forms confused under the name *Aspergillus glaucus*, securing 23 collections from various sources and subjecting them to comparative study under various conditions. Their reactions to different temperatures and to different nutrient solutions enabled him to separate the forms into few groups, the reactions of whose

[15] THOM, CHARLES, Cultural studies of species of *Pencillium*. Bur. Animal Ind. Bull. 118. pp. 109. 1910.

[16] MANGIN, L., Qu'est-ce que l'*Aspergillus glaucus?* Ann. Sci. Nat. Bot. IX. 10:303–371. *figs. 15.* 1909.

members were constant for the same media or temperatures. He shows that characters of the conidia are not sufficiently constant for the differentiation of species; the form and dimensions of the ascospores, however, are useful as diagnostic characters of species. Four species confused by authors as *Aspergillus glaucus* are described and figured; two of these are new. A variety *violaceum* is added under *Eurotium herbariorum*, and characters are given to separate these forms from two other members of the same group, *A. Oryzae* and *A. flavus*.—H. HASSELBRING.

Fossil Osmundaceae.[17]—In this final contribution on the fossil Osmundaceae, the authors bring to a conclusion their investigations and summarize their results for the whole series. The present memoir deals with a new stem, *Osmundites Kolbei*, from the Jurasso-Cretaceous (Wealden) of Herbertsdale, Cape Colony. The softer tissues are stated to be almost entirely destroyed before fossilization, so that only the fibrovascular and scelerenchymatous systems are left. The stem is much flattened and generally in a condition of extreme collapse. The authors state that the fibrovascular ring is so much flattened that the opposite sides are sometimes in contact with each other. They omit to state, a matter of the utmost importance in connection with their conclusions, clearly shown by their fig. 1, that the condition of maceration is so extreme that the central cylinder has not only collapsed but has been burst open and distributed throughout the cross-section of the stem. It is not surprising, in view of the extreme decay and displacement presented by their material, that they find tracheids and masses of tracheids scattered in the central substance lying in the midst of the displaced fibrovascular strands. The authors express the conviction "that there is no doubt that the tracheal elements are true and real constituents of the central tissue." It is unfortunate that they have not demonstrated the accuracy of their interpretation by figures of transverse sections on a sufficient scale of magnitude of the stelar tissues. An unprejudiced anatomist would scarcely admit the accuracy of their statements on the evidence they submit. From this highly disintegrated stem it is not surprising, in view of their previous statements, that they draw the conclusion that the central tissue of the osmundaceous stele was originally composed of tracheids, and that hence the pith in this family is a derivative of the fibrovascular tissues. The authors make the discovery, anticipated by Mr. SINNOTT in the case of the living Osmundaceae, that foliar gaps apparently absent in *Osmundites Kolbei* are in reality present. Finally, they draw up a table of the osmundaceous forms investigated by them, which shows clearly that the protostelic representatives are of more ancient origin, so far as the available geological record goes, than whose with a developed pith. Their reasoning in regard to the medullate forms is not so conclusive, since they mention three species, *O. Gibbiana*, *O. Kolbei*, and *O. skidegatensis*, from not very

[17] KIDSTON, R., and GWYNNE-VAUGHAN, D. T., Fossil Osmundaceae. IV. Trans. Roy. Soc. Edinburgh **47**[3]:no. 17. 1910.

different geological levels, Lower Cretaceous and Upper Jurassic, as proving their hypothesis that the pith of the Osmundaceae is of stelar origin and that the medullate forms are an ascending series, beginning with species which have a pith but no foliar gaps separating the collateral bundles, and ending with those in which the bundles are concentric and separated by widely patent gaps. So far as the testimony goes, which they have brought forward in their various memoirs, this hypothesis appears to bear a surprising resemblance to a confession of faith, since it is essentially the substance of things not seen but hoped for.—E. C. JEFFREY.

Parasites and xeno-parasites.—The extensive investigations of CANNON[18] upon the root habits of desert plants has added *Orthocarpus purpurascens* and two species of *Krameria* to the list of semiparasitic plants. *Orthocarpus*,[19] the first to be reported, is an annual of small size, united by its roots to a considerable variety of hosts, of which most are also annual in habit. *Krameria canescens* and *K. parvifolia*, two shrubby desert plants, were formerly taken to be autophytic, and the present study seems to show that they have not advanced far in parasitism. The seeds germinate readily irrespective of the presence or absence of the host plants, and the seedlings are capable of independent existence for an indefinite period, and yet when associated with possible hosts the root tips of *Krameria* organize haustoria penetrating the roots of the host and forming therewith close vascular connections. *Krameria parvifolia* has been found on *Parkinsonia microphylla* only, but *K. canescens* has a variety of hosts, being most frequently associated with *Covillea tridentata*. These parasites show but few of the atrophies or alterations usually accompanying dependent nutrition.

In making a study of the conditions which may have led to the development of parasitism, MACDOUGAL[19, 20] has succeeded in uniting various plants, so that the one lived parasitically upon the other for more than two entire seasons. Various species of cactus were usually chosen as hosts, *Echinocactus* and the giant *Cereus* figuring most conspicuously in this rôle, while the "xeno-parasites" included the Mexican grape, agave, various cacti, and other succulent plants. After the union of the host and parasite was effected, there appeared in the development of the latter the atrophies and reductions characteristic of parasites. It appears that the relative acidity of the sap of the two plants has no part in determining their potentialities as parasite and host, but for the one to draw its nutrition from the other the latter must possess sap of a lower osmotic activity than the former, although not all plants thus related

[18] MACDOUGAL, D. T., and CANNON, W. A., The conditions of parasitism in plants. Publication no. 129, Carnegie Institution of Washington. 1910.

[19] CANNON, W. A., Parasitism of *Orthocarpus purpurascens*. Plant World **12**: 259–261. 1909.

[20] MACDOUGAL, D. T., The making of parasites. Plant World **13**: 207–214. 1910.

are capable of symbiosis, there being other unknown limiting factors.—GEO. D. FULLER.

Fertile and sterile strains of Hymenomycetes.—Miss WAKEFIELD[21] has made a study of the conditions influencing the formation of fruit-bodies of *Schizophyllum commune* and *Stereum purpureum*, which were grown in pure cultures on bread and gelatin or agar media. The most interesting fact brought out by the work is that a disposition or tendency to form fruit-bodies is characteristic of certain strains, while others have a strong tendency to remain sterile. Of thirteen colonies of *Schizophyllum commune* obtained from single spores from various sources, two formed fruit-bodies readily, while the others remained sterile or showed only a slight tendency to fruit. When propagated by the transplanting of bits of mycelium to new nutrient media, the strains maintained their peculiar characteristics with regard to fruiting. *Stereum purpureum* behaved in a similar manner. Although the capacity for fruiting is thus a characteristic predetermined in the spore, the actual production of fruit-bodies is dependent upon certain internal conditions which were studied to some extent. In a moist atmosphere, depressing transpiration, only vegetative growth appears. Absence of light also is said to inhibit the formation of normal fruit-bodies in *Schizophyllum*. Certain other factors appear to act as direct "releasing stimuli." Thus the sudden withdrawal of nutriment leads to the production of fruit-bodies. Even some of the sterile strains show a tendency to fruit under proper conditions of transpiration and nutrition, indicating that the line between sterile and fertile strains may be after all largely a matter of response to environment.—H. HASSELBRING.

Sand dunes of New Zealand.—In preparation for efforts at dune reclamation, COCKAYNE[22] has prepared a report upon the sand dunes of New Zealand. They cover an area of over 500 square miles, with a general height of 20–50 feet, but occasionally attaining a maximum height of 300 feet. A general summary of their geological character and history is followed by a consideration of the disturbing effect of man's burning and grazing operations. Many dunes that had long been entirely fixed have thus been revivified by advancing civilization. A discussion of the ecological factors involved brings to light the interesting conclusion that the amount of precipitation affects the dune flora very little, areas with an annual rainfall of 100 inches having the same vegetation as others with only 25 inches. A very large number of cloudy and rainy days, however, does modify the xerophytic character of the dune plant associations. The sand-building and sand-collecting plants are

[21] WAKEFIELD, MISS E., Ueber die Bedingungen der Fruchtkörperbildung, sowie das auftreten fertiler und steriler Stämme bei Hymenomyceten. Naturwiss. Zeitschr. Forst. u. Landwirtsch. **7**:521–551. *figs.* 3. 1909.

[22] COCKAYNE, L., Report on the sand dunes of New Zealand. Department of Lands, Wellington, N.Z. pp. 30. *pls.* 35. 1909.

all species peculiar to New Zealand, but familiar genera such as *Scirpus*, *Festuca*, *Calamagrostis*, and *Euphorbia* are conspicuous. The "sandgrass" dunes and the shrub dunes represent the chief dune plant associations, the almost entire absence of forests being noticeable. A bibliography of the literature relating to the New Zealand dunes completes the interesting report.—GEO. D. FULLER.

Isolated ovulate plants of Mercurialis.—In a recent paper on the determination of sex[23] STRASBURGER described the behavior of isolated ovulate plants of *Mercurialis annua*. The subsequent behavior of these plants is now described.[24] They remained sterile for months, then formed staminate flowers and began to fruit. The pollen of staminate flowers is shed immediately when the anthers dehisce, and the flower drops off the next day, so that they might easily escape observation. Isolated sterile ovulate plants, when pollinated with the pollen of staminate individuals, produce staminate and ovulate plants in about equal numbers; but when pollinated with pollen from the scattered staminate flowers of ovulate plants, the resulting plants are almost exclusively ovulate. When ovulate plants have been pollinated with pollen from a staminate individual and have fruited, they begin to produce scattered staminate flowers. The haploid number of chromosomes, as counted in the pollen mother cells, is 7, and the diploid, both in young embryos and older plants, is 14. There are no adventitious embryos. Both in the observations and in the discussion of the results, this paper adds to STRASBURGER's already important contributions to the problem of the determination of sex.—CHARLES J. CHAMBERLAIN.

Coastal deserts of Jamaica.—Studying the south coast of Jamaica, SHREVE[25] has explained the desert-like character of an area extending some 70 miles west of Kingston as edaphic areas of desert in a savanna region. The rainfall, 32 inches a year, is capable of supporting a savanna where the soil is deep, the desert being sharply confined to limestone areas with very thin soils and an extremely rough surface. The use of the porous cup atmometer shows an evaporation similar to that of the humid coastal regions in the subtropical United States and much less than that of the inland desert region. The vegetation, however, closely resembles that of the continental desert, being characterized by various species of *Acacia*, *Cassia*, *Cereus*, and *Opuntia*. Bordering the desert there is often a zone of thorn forest, made up almost exclusively of *Prosopis juliflora*. Similar deserts result from similar factors on the coasts of Cuba, San Domingo, and many of the smaller West Indian islands.—GEO. D. FULLER.

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[23] Review in BOT. GAZETTE **48**:63. 1909.

[24] STRASBURGER, E., Das weitere Schicksal meiner isolierten weiblichen *Mercurialis annua*-Pflanzen. Zeitschrift für Botanik **1**:507–524. *pl. 14*. 1909.

[25] SHREVE, FORREST, The coastal deserts of Jamaica. Plant World **13**:129–135. 1910.

Embryos of Angiopteris and Kaulfussia.—In connection with a study of these two genera, CAMPBELL[26] has presented the embryo-formation of Marattiaceae. He thinks it probable that in all cases the stem, leaf, and root are epibasal in origin. In *Danaea* the primary hypobasal cell forms a suspensor, so that the foot also is epibasal; and in *Kaulfussia* and *Angiopteris* the foot is also partly epibasal in origin. The root arises endogenously as a secondary structure, and in its growth almost obliterates the foot, which is very large in the young embryo.—J. M. C.

Anatomy of Calamostachys.—HICKLING[27] has studied new sections of *C. Binneyana*, and has come to the conclusion that the so-called fertile or sporangiophore-bearing "nodes" are not nodes in the same sense as the bract-bearing nodes. He shows that the sporangiophore trace arises from the node that supplies the whorl of bracts below, and he believes this to be a general characteristic of calamitean strobili, the point of insertion of the sporangiophores on the internode being very variable.—J. M. C.

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[26] CAMPBELL, D. H., The embryo and young sporophyte of *Angiopteris* and *Kaulfussia*. Ann. Jard. Bot. Buitenzorg II. Suppl. III. pp. 69–82. *pls. 6, 7*. 1909.

[27] HICKLING, GEORGE, The anatomy of *Calamostachys Binneyana* Schimper. Mem. and Proc. Manchester Lit. and Phil. Soc. **54**:no. 17. pp. 16. *pl. 1*. 1910.

GENERAL INDEX

Classified entries will be found under Contributors and Reviews. New names and names of new genera, species, and varieties are printed in **bold face** type; synonyms in *italic*.

A

Abrams, L., work of 232
Absorption, ratio of phosphate, nitrate, and potassium on 1; of salts by Bromeliaceae 160
Achlya **caroliniana** 381
Adoxa moschatellina, morphology of 154
Agave, Trelease on 71
Alangium 471
Albuminous cells of ray tracheids 111
American Breeders' Magazine 315
American Naturalist 314
Ames, O., work of 232
Ammonium salts, rôle of 75
Amyris 233
Anatomy 470; of Calamostachys 480
Andrews, F. M. 193
Andrews, L., work of 231
Angiosperms, embryo of 480
Anguilla, flora of 232
Antheridia, of ferns 52
Anthers, dehiscence of 158
Apogamy, Burmannia 76; ferns 53; Pteris 239; Trichomanes 80
Apospory, Trichomanes 80
Appel, O., work of 158
Appleman, C. O. 150, 182
Araceae 233
Araucarineae and Podocarpineae 92
Araucariopitys 70
Arber, Agnes, work of 397
Archegonia, of ferns 52
Archiv für Kassen- und Gesellschafts-Biologie 314
Ascocarp of Leotia 443
Aspergillus 474
Aso, K., work of 160
Atkinson, G. F. 220
Atmograph 214

B

Bach, A., work of 151
Bacteria, hydrogen 77; iron 464
Bacteriology, outlines of 229
Bahamas, naturalist in 390
Baicalia 233
Bailey, I. W. 142, 374; work of 236
Bancroft, C. K., work of 472
Bartlett, A. W., work of 473
Bastardiopsis 232
Bateson, W., work of 228
Bennettitales 74
Berry, E. W. 202, 305
Beutenmuller, Wm., work of 240
Billings, F. H., work of 395
Biometrika 313
Bissell, C. H., work of 231
Blackman, F. F., work of 234
Blake, S. F., work of 232
Blanchetiastrum 232
Blodgett, F. H. 340
Børgesen, F., work of 232
Boldingh, I., work of 232
Bolivia, plants of 232
Boodle, L. A., work of 69
Boraginaceae 233
Botanical Congress at Brussels 220
Bovie, W. T., work of 237
Bower, F. O., work of 238
Brachyphyllum 68
Brazinski, J., work of 393
Bromeliaceae, absorption of salts 160
Brooks, M. A., work of 236
Brooks, F. T., work of 473
Brown, W. H. 443
Bruchmann, H., work of 391
Bulbs of Erythronium 340
Burseraceae 232
Burgeff, H., "Die Wurzelpilze der Orchideen" 386
Burmannia coelestis, apogamy in 76
Burret, M., work of 232

C

Calamostachys, anatomy of 480
Caldwell, O. W. 310, 311
Callitris, morphology of 397
Campbell, D. H., work of 320, 480
Cannon, W. A., work of 477
Carbon dioxid as a fertilizer 398
Carex 233
Catalase, observations on 182
Catathelasma 383; **evanescens** 384
Cedroxylon 70
Cercis, length of pod and fertility 117
Chabaud, B., work of 232

Chamberlain, C. J. 67, 72, 76, 79, 155, 160, 318, 415, 479; and Coulter, J. M., "Morphology of gymnosperms" 466
Chemotropism of roots 71
Chilean fungi 430
Chlorophyceae, new genera of 399
Christ, H., "Die Geographie der Farne" 312; work of 232
Chromocrea 233
Chromocreopsis 233
Chromosomes, differentiation among 72; microchemistry of 160
Cladosporium 472
Clapp, Grace L. 386, 392
Clark, C. F., work of 392
Clark, G. H., and Fletcher, J., "Farm weeds of Canada" 389
Clavaria **truncata** 385
Claviceps 460; **Paspali** 462; **Rolfsii** 462; **Tripsaci** 463
Clityocybe **pruinosa** 384
Coastal deserts of Jamaica 479
Cockayne, L., work of 478
Cogniaux, A., work of 232
Coker, W. C. 381
Colloidal chemistry 151
Collybia maculata **moschata** 384
Compositae 233
Compression, and mechanical tissue 257
Congo, flora of 471
Conifers, bars of Sanio 78; classification 318; ecology 394; fossil 75; ray tracheids 101
Connecticut plants, catalogue of 231
Contributors: Andrews, F. M. 193; Appleman, C. O. 150, 182; Atkinson, G. F. 220; Bailey, I. W. 142, 374; Berry, E. W. 202, 305; Blodgett, F. H. 340; Brown, W. H. 443; Caldwell, O. W. 310, 311; Chamberlain, C. J. 67, 72, 76, 79, 155, 160, 318, 415, 479; Clapp, Grace L. 386, 392; Coker, W. C. 381; Cook, Mel. T. 152, 240; Coulter, J. M. 78, 79, 80, 235, 236, 238, 239, 240, 320, 380, 390, 395, 397, 398, 399, 470, 471, 472, 480; Cowles, H. C. 312, 394, 468; Crocker, William 73, 75, 77, 78, 154, 155, 159, 230, 233, 234, 237, 238, 240, 312, 315, 317, 320, 321, 398; Eikenberry, W. L. 214; Farlow, W. G. 220; Fuller, G. D. 389, 477, 478, 479; Greenman, J. M. 231, 232, 470, 472; Hall, J. G. 460; Harris, J. A. 117; Harris, N. M. 229, 464; Hasselbring, H. 65, 153, 157, 158, 472, 474, 478; Howe, R. H., Jr. 159; Jeffrey, E. C. 67, 69, 70, 74, 75, 318, 319, 401, 466; Knight, L. I. 321; Land, W. J. G. 77; Lewis, I. F. 59; Livingston, B. E. 151, 242; Lovejoy, Ruth H. 383; Mottier, D. M. 209; Pace, Lula 49; Pennington L. H. 257; Pond, R. H. 158, 398, 399; Pool, Venus W. 159; Riddle, L. W. 285; Roberts, Edith 321; Rose, R. C. 71, 73, 76, 156, 159, 160; Saxton, W. T. 31; Schreiner, Oswald 1, 161; Shull, G. H. 226, 313, 392, 393, 395; Sister Helen Angela 396; Skinner, J. J. 1, 161; Smith, F. Grace 128; Stevens, F. L. 460; Stokey, Alma G. 218; Thaxter, Roland 430; Thompson, W. P. 101; Thomson, R. B. 148; Wilcox, E. Mead 240; Young, Mary S. 81, 236
Cook, Mel. T. 152, 240; work of 400
Cordaitales 78
Cornus 471
Correlation 271; in oats 395
Costa Rica, ferns of 232
Cotyledons, removal of 240
Coulter, J. M. 78, 79, 80, 235, 236, 238, 239, 240, 320, 380, 390, 395, 397, 398, 399, 470, 471, 472, 480; work of 72; and Chamberlain, C. J., "Morphology of gymnosperms" 466
Cowles, H. C. 312, 394, 468
Crepis virens, chromosomes of 72
Cretaceous, pine leaves 319; plants of Japan 67
Cretovarius 68
Crocker, William 73, 75, 77, 78, 154, 155, 159, 230, 233, 234, 237, 238, 240, 312, 315, 317, 320, 321, 398
Cryptomeriopsis 68
Cucurbitaceae, peg of 321
Cunninghamia, morphology of 240
Cuphea 232
Czapek, F., work of 234

D

Davis, J. J., work of 80
DeFraine, E., work of 239
Degenia 232
Delphinium 233
Desert vegetation and soil moisture 241
Dictyota, periodicity in 59
Dioon edule, fertilization and embryogeny 415
Diseases 65, 472; apple 240; smuts 158, 159
Drude, O., and Engler, A., "Vegetation der Erde" 468
Duggar, B. M., "Fungus diseases of plants" 65
Dunes of New Zealand 478
Durand, Théoph. et Hél., "Florae Congolanae" 471

E

Eames, E. H., work of 231
Ecology of conifers 394
Eikenberry, W. L. 214
Ellis, D., "Outlines of bacteriology" 229
Embryo, Angiopteris 480; Dioon 415; Kaulfussia 480; Labiatae 395; Phyllocladus 87; Widdringtonia 40
Embryo sac, Fritillaria 400; Onagraceae 79; Pandanus 320
Endophyton 399
Engler, A., "Das Pflanzenreich" 470; and Drude, O., "Vegetation der Erde" 468; work of 232
Entoloma viridans 385
Enzymes, in sap stain 142
Eocene flora in Georgia 202
Ernst, A., work of 76, 160
Erythronium, bulbs of 340
Eucalyptus, revision of 472
Euphorbiaceae 233
Excretion of salts, in Statice 159
Evolution of plants 236
Ewert, R., work of 473

F

Fagoxylon 68
Farlow, W. G. 220
Farm weeds 389
Fawcett, W., work of 232
Female gametophyte, Phyllocladus 85; Zamia 135
Fermentation, alcoholic 154
Ferns, antheridia 52; apogamy 53; archegonia 52; gametophyte 49; fertilization 53
Fertilization, Dioon 415; ferns 53
Filicales, phylogeny of 238
Fitting, H., work of 76
Flagellates, new genus of 399
Fletcher, J., and Clark, G. H., "Farm weeds of Canada" 389
Florideae 232
Frenelopsis, epidermal characters of 305
Freundlich, H., "Kapillarchemie" 151
Freund, Yella, work of 240
Fritillaria, two embryo sacs in 400
Fujii, K., work of 67
Fuller, G. D. 389, 477, 478, 479
Fungi, Chilean 430; on Euphorbia 233; parasitic, of Wisconsin 80; Philippine 233

G

Galitzky, Katherine, work of 317
Galls, insect 240; of Michigan 400; Stebbins on 152
Galtonia candicans, root tips and temperature 73
Gametophyte, fern 49; sex in Onoclea 209; Widdringtonia 34, 37
Ganong, W. T., "Teaching botanist" 310
Gardner, N. L., work of 399
Garrya 471
Gates, R. R., work of 79
Genetics, magazines 313
Georgevitch, Peter, work of 73, 80
Geotropism 155, 317; and split stems 238
Gerry, Eloise, work of 78
Gilg, E., work of 232
Giltay, E., work of 155
Gleichenia, vascular anatomy 69
Gloeophyllum ferrugineum 385
Gnetales, seedling structure of 239
Gothan, W., work of 70
Graves, C. B., work of 231
Greene, E. L., work of 232
Greenman, J. M. 231, 232, 470, 472
Grewia 232
Groom, Percy, work of 394
Growth, ratio of phosphate, nitrate, and potassium on 1
Guttenberg, H. R. v., work of 317, 318
Gwynne-Vaughan, D. T., work of 74, 476
Gymnosperms, morphology of 466; vascular plate and cotyledons of 72

H

Hall, J. G. 460
Hannig, E., work of 158
Harger, E. B., work of 231
Harris, J. Arthur 117
Harris, N. M. 229, 464
Hasselbring, H. 65, 153, 157, 158, 472, 474, 478
Hassler, E., work of 232
Hayek, A. von, work of 232
Helichrysum 233
Heller, A. A., work of 232
Helminthostachys, suspensor of 400
Heliotropism 317
Heredity 226; and variation 270
Hickling, George, work of 480
Hiley, W. E., work of 69
Hill, T. G., work of 239
Holleman, A. F., "Organic chemistry" 312
Hormodendron 472
Howe, R. H., Jr. 159; work of 232
Hydrocyanic acid, rôle of 156
Hymenomycetes, fertile and sterile strains 478
Hypocreales 233

I

Illinois State Academy of Science 472
Indigofera campestris 232
Insect galls 240; of Michigan 400; Stebbins on 152
Iron bacteria 464

J

Jacobi, Helene, work of 240
Jamaica, coastal deserts of 479
Japan, cretaceous plants of 67
Jatropha 471
Jeffrey, E. C. 67, 69, 70, 74, 75, 318, 319, 401, 466
Jensen, P. B., work of 320
Johannsen, W., "Elemente der exacten Erblichkeitslehre" 227
Jongmans, W. J., "Palaeobotanische Literatur" 471
Jugloxylon 68
Jurassic, flora of Normandy 80; woods 70

K

Kastle, J. H., "The oxidases" 150
Kaulfussia, embryo of 480
Kershaw, F. M., work of 319
Kidston, R., work of 74, 476
Knight, Lee I. 321
Koehne, E., work of 232
Kohl, F. G., work of 154
Kooper, W. D., work of 399
Kraemer, Henry, "Text-book" 390
Kränzlin, F., work of 233
Krause, K., work of 233
Kükenthal, G., work of 233
Kuijper, J., work of 233

L

Labiatae, embryo 395
Lagerberg, T., work of 154
Land, W. J. G. 77
Lang, W. H., work of 400
Lawson, A. A., work of 235
Leaves, periodicity in nitrogen 399
Leavitt, S., work of 153
Lebedeff, A. J., work of 77
Lechmere, A. E., work of 400
LeClerc, J. A., work of 153
Leeuwen-Reijnvaan, Drs. Van, work of 77
Leotia, ascocarp of 443; chlorocephala 447; lubrica 443
Lewis, C. E., work of 240
Lewis, I. F. 59
Lignier, Octave, work of 80
Lingelsheim, A., work of 232
Livingston, B. E. 151, 242
Loesener, Th., work of 233
Lovejoy, Ruth H. 383
Lycopodium, prothallia 301; sporangia 218; tristachyum 232.
Lychnis, Shull on color inheritance in 79

M

McAlpine, D., work of 474
McDougal, D. T., work of 477
Maiden, J. H., "Revision of Eucalyptus" 472
Male gametophyte of Phyllocladus 82
Mangin, L., work of 475
Marckea 232
Maslen, A. J., work of 78
McCallum, W. H., work of 240
Mechanical tissue, and longitudinal compression 257
Megabaria 253
Mendel Journal 314
Mercurialis, ovulate plants of 479
Meyer, Arthur, work of 73
Michigan, insect galls 400
Microtome for cutting wood 148
Mitrospermum, structure of 397
Mitscherlich, E. A., work of 398
Miyake, K., work of 240
Mnium, spermatogenesis in 77
Modilewski, J., work of 79
Moeser, W., work of 233
Molds, source of nitrogen 159
Molisch, H., "Eisenbakterien" 464
Morphology of plants 67
Mottier, D. M. 209

N

Nathorst, A. G., work of 74, 75
National Academy of Sciences 71
Němec, B., work of 160
Neojatropha 471
New Zealand, dunes of 478
Niponophyllum 68
Nitrogen, periodicity in leaves 399; source of, for molds 159
Nitrate, ratio of, on absorption and growth 1
Nordhausen, M., work of 398
Normandy, Jurassic flora of 80
North American Flora 231
Northrop, J. I., memorial volume 390

O

Oats, correlation in 395
Oak woods 374
Oenothera, Lamarckiana, the original 79; twin hybrids 193

Onoclea, sex of gametophyte 209
Orchids 232, 233; flowers, formative stimuli 76; root-fungi 386
Osborne, T. B. "The vegetable proteins" 230
Osmundaceae, fossil 74, 476
Oxidases 150
Oxytropis 233
Otto, R., work of 399
Ovule, Zamia 128

P

Pace, Lula 49
Palibine, J. W., work of 233
Palladin, W., work of 315, 316
Pandanus, embryo sac of 320
Paleobotanical literature 471
Parasites 477
Pax, F., work of 232, 233, 469, 471
Peg of Cucurbitaceae 321
Penicillium 474
Pennington, L. H. 257
Permeability 234
Petersen, H. E., work of 233
Pflanzenreich 470
Pharmacognosy, text-book of 390
Phosphate, ratio of, on absorption and growth 1
Phototropism 398
Phyllocladoxylon 70
Phyllocladus, embryo 87; female gametophyte 85; male gametophyte 82; morphology 82; relationship 91
Phylloglossum, morphology of 318
Physcia villosa 159
Pilger, R., work of 233
Pinus, evolution of 236
Pityoxylon 70
Podocarpineae, and Araucarineae 92; morphology of 81
Podocarpus, structure of 236
Polarity 240
Pond, R. H. 158, 398, 399
Pool, Venus W. 159
Populocaulis 68
Porodoko, Theodor, work of 71
Potassium, ratio of, on absorption and growth 1
Prianischnikow, D., work of 75
Protopiceoxylon 70
Proteases, Vines on 78
Protein, vegetable 230
Prothallium of Lycopodium 301
Psilotum, morphology of 239
Pteris, apogamy in 239
Pteropsida 401
Pulle, A., work of 233
Pythiomorpha 233

Q

Queva, C., work of 396

R

Rafflesia, fertilization in 160
Ray tracheids, albuminous cells of 11; in Coniferae 101; in roots 102
Rendle, A. B., work of 232
Respiration 233, 315
Reviews: Burgeff's "Die Wurzelpilze der Orchideen" 386; Christ's "Geographie der Farne" 312; Clark and Fletcher's "Farm weeds of Canada" 389; Coulter and Chamberlain's "Morphology of gymnosperms" 466; Duggar's "Fungous diseases of plants" 65; Durand's "Florae Congolanae" 471; Ellis' "Outlines of bacteriology" 229; Engler's "Pflanzenreich" 470; Engler and Drude's "Vegetation der Erde" 468; Fletcher and Clark's "Farm weeds of Canada" 389; Freundlich's "Kapillarchemie 151; Ganong's "Teaching botanist" 310; Holleman's "Organic chemistry" 312; Johannsen's "Elemente der exacten Erblichkeitslehre" 227; Jongmans' "Palaeobotanische Literatur" 471; Kastle's "Oxidases" 150; Kraemer's "Text-book" 390; Maiden's "Revision of Eucalyptus" 472; Molisch's "Eisenbakterien" 464; Osborne's "Vegetable proteins" 230; Stevens' "Plant anatomy" 470; Velenovský's "Morphologie der Pflanzen" 67; Willis' "Agriculture in the tropics" 311
Richter, O., work of 317
Riddle, L. W. 285
Ritchieophyton 471
Ritter, G., work of 159
Roberts, Edith 321
Robinson, C. B. work of 233
Root, chemotropism of 71; ray tracheids in 102
Root-fungi of orchids 386
Rorhardt, P. A., work of 238
Rosenberg, O., work of 72
Rose, R. C. 71, 73, 76, 156, 159, 160
Rydberg, P. A., work of 233

S

Sabal uresana 232
Sabiocaulis 68
Sackett, W. C., work of 159
Sap, rise of 238; stain, oxidizing enzymes 142
Saxegothaea, morphology of 94

Saxton, W. T. 31; work of 397
Schmidt, Ernst, work of 73
Schreiner, Oswald 1, 161
Schtscherback, Johann, work of 159, 238
Sciadopitys, morphology of 235
Scion and stock, interaction between 73
Scirpodendron 232
Scott, D. H., work of 78
Seaver, F. J., work of 233
Seedling, of Gnetales 239; of Trapa 396
Selaginella, sporophylls of 396
Sex, in gametophyte of Onoclea 209
Shreve, Forrest, work of 479
Shull, G. H. 226, 313, 392, 393, 395; work of 79
Sister Helen Angela 396
Skinner, J. J. 1, 161
Smith, F. Grace 128
Smuts, treatment for 158
Soil, a harmful organic constituent 161; moisture and desert vegetation 241
Spermatogenesis in Mnium 77
Sporangium of Lycopodium 218
Sporophylls of Selaginella 396
Statice, excretion of salts 159
Stebbins, Fannie A., work of 152
Stephens, E. L., work of 239
Stereocaulon, albicans 303; alpinum 298; condensatum 290; coralloides 291; denudatum 300; nanodes 303; North American species 285; paschale 292; pileatum 289; ramulosum 304; tomentosum 296; tomentosum **simplex** 298; Wrightii 302
Stevens, F. L. 460
Stevens, W. C., "Plant anatomy" 470
Stiles, W., work of 236, 239, 396
Stimulus, conduction of 320; formative 76
Stock and scion, interaction between 73
Stokey, Alma G. 218
Stopes, Marie C., work of 67, 319
Strasburger, E., work of 479
Strobilus, of Widdringtonia 31; of Zamia 128
Surinam, flora of 233
Suspensor, in Helminthostachys 400
Sydow, H., work of 233
Sydow, P., work of 233
Sykes, M. G., work of 239, 396

T

Tahara, M., work of 72
Taphrina **entomospora** 437
Taxonomic literature 232
Temperature, and living cells 73
Timothy, variation in 392
Thaxter, Roland 430
Thom, Charles, work of 475
Thompson, W. P. 101
Thomson, R. B. 148
Transpiration organs 237
Tranzschel, W., work of 233
Trapa, seedling of 396
Traumatic woods 374
Trelease, William, work of 71
Trichomanes, apospory and apogamy in 80
Twin hybrids, anatomical distinctions 193

U

Uncinula **magellanica** 440; **Nothofagi** 439
Usnea 232

V

Valeriana 233
Variation 270
Vascular anatomy, Gleichenia 69
Vegetable protein 230
Vegetation der Erde 468
Velenovský, Jos., "Morphologie der Pflanzen" 67
Vernon, H. M., work of 78
Vierhapper, E., work of 319
Vines, S. H., work of 78

W

Wakefield, E., work of 478
Waldron, L. R., work of 395
Wangerin, Walter, work of 470
Wassiljeff, Vera, work of 317
Water, non-available 237
Weatherby, C. A., work of 231
Weeds, farm 389
Wernham, H. F., work of 318
Wheat, influence of environment 153
Whetzel, H. H., work of 159
Widdringtonia, cupressoides, life history of 31; embryo of 40; gametophytes of 34, 37
Wilcox, E. Mead 240
Willis, J. C., "Agriculture in the tropics" 311
Wilson, M., work of 77
Wilson, P., work of 233
Winkler, H., work of 232
Wisconsin, parasitic fungi of 80
Wood, traumatic oak 374
Wooton, E. O., work of 233
Worsdell, W. C., work of 398

X

Xeno-parasites 477
Xenoxylon 70

Y

Yezonia 68
Young, Mary S. 81, 236

Z

Zamia, female gametophyte 135; ovulate strobilus 128; ovule 128
Zanthoxylum 233
Zeitschrift für induktive Abstammungs- und Vererbungslehre 314
Zijlstra, K., work of 237